Age, growth, and reproduction of Southern Kingfish (*Menticirrhus americanus*): a multivariate comparison with life history patterns in other sciaenids

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Abstract—Southern Kingfish (*Menticirrhus americanus*) is an abundant sciaenid in the northcentral Gulf of Mexico, but little is known of its life history. Our objectives were to describe demographic traits and compare the characteristics of this population with those of other recreationally and commercially important populations in the U.S. Exclusive Economic Zone (U.S. EEZ). We report significant differences in sex-specific weight at length. Otolith annulus formation occurred in April and May and maximum age was 4+ years for both sexes. Length-at-age analysis indicated that mean asymptotic total length (TL; $TL_{\infty, male}$=244 mm, $TL_{\infty, female}$=303 mm) and mean instantaneous growth rates (k_{male}=1.12 y^{-1} and k_{female}=0.95 y^{-1}) were significantly different between sexes. The mean length at 50% maturity (TL_{50}) for females was 171 mm TL, corresponding to an age at maturity of 1 year. Gonadosomatic indices and histological examination of ovarian maturity phases indicated rapid gonadal development in February and March with females actively spawning from April to September. The interval between spawning averaged 6.9 days, and the most frequent spawning occurred in June and July. Mean relative batch fecundity was 231.1 number of eggs g^{-1} of ovary-free body weight (±standard error 35.7). Principal component analysis (PCA) of 5 variables from 17 sciaenid populations in the U.S. EEZ identified 2 principal components that explained 68.1% of variation among populations; these components represent a size-related gradient and a gradient of spawning season dynamics. Five distinct groups were identified on the basis of fish size, age at maturity, spawning-season duration, and batch fecundity.

The family Sciaenidae include many commercially and recreationally important species and occur worldwide in temperate and subtropical marine, estuarine, and fresh waters (Chao, 1995, 2002). There are 79 sciaenids that occur in North America (Page et al., 2013); 36 of these species commonly occur in waters of the U.S. Exclusive Economic Zone (U.S. EEZ), and 29 of those 36 species support either commercial or recreational fisheries or both (FishBase, http://www.fishbase.org). However, only 11 of these fishes are reported individually in the NOAA National Marine Fisheries Service commercial (http://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/annual-landings/index, accessed September 2013) and recreational (http://www.st.nmfs.noaa.gov/st1/recreational/queries/catch, accessed September 2013) statistics databases. Despite the conspicuousness of this family, complete life-history information is not available for many of the commonly occurring species, including some economically important members.

Understanding life-history strategies and the interaction among species traits, environmental factors, and population dynamics is not only important for fisheries management but also vital to predict population responses to a variety of natural and anthropogenic disturbances (Winemiller and Rose, 1992; Winemiller, 2005). A comparison of life-history traits of species within the single, diverse family Sciaenidae can further the understanding of the dynamics of this valuable group of fishes. For example, analysis of the reproductive life-history traits of Sciaenidae in the Gulf of Mexico (GOM) and Caribbean Sea resulted in the recognition of 3 major groups within this family that were defined by maximum length, fecundity, and duration of spawning season (Waggy et al., 2006). Similarly, Militelli et al. (2013) recently examined reproductive traits of 7 sciaenids from the Buenos Aires, Argentina, coastal zone and found that composite groups could be described on the basis of the length of the reproductive period and size of the spawning area.

Life-history patterns of many of the Sciaenidae in the northcentral GOM are not well understood, and limited life-history information is available on the *Menticirrhus* complex, which includes Gulf Kingfish, (*Menticirrhus littoralis*), Northern Kingfish (*M. saxatilis*)*,* and Southern Kingfish (*M. americanus*). These species are targeted by both recreational and commercial fishermen in Mississippi, and all of them currently are unregulated in the northcentral GOM. Results from analysis of NOAA harvest data for 2000–11 indicate a decline in annual landings of Southern Kingfish from 117,967 to 36,332 kg in Mississippi waters during this time period (http://www.st.nmfs.noaa.gov/st1/recreational/queries/catch, accessed September 2013). This decline likely was affected by a number of factors, and it may be cause for concern for the sustainability of the population.

Southern Kingfish is a widely distributed estuarine sciaenid with a range in coastal waters from southern New England to the southern tip of Florida, the GOM and Caribbean Sea, and as far south as Argentina (Armstrong and Muller[1]; Chao, 2002; Haluch et al.*,* 2011; Militelli et al., 2013); it is the most commonly occurring *Menticirrhus* species in northcentral GOM waters. Although most frequently encountered over sandy bottoms (Chao, 2002), this species has been found in deep channels between barrier islands generally over sand, in shallow muddy bottoms, in seagrasses, or on shell hash (Reid, 1954; Bearden, 1963; Crowe, 1984). Seasonal movements of Southern Kingfish appear to occur from shallow waters, where it occurs in early spring through late fall, to deeper waters during the winter (Hildebrand and Cable, 1934; Bearden, 1963; Lagarde[2]; Fritzsche and Crowe[3]; Crowe, 1984)**.**

Updated information on age, growth, and reproduction of Southern Kingfish in the middle South Atlantic Bight (SAB) was published last year (McDowell and Robillard, 2013) and includes the first age estimates from otoliths and fecundity estimates. However, similar current information, including histological assessment, for Southern Kingfish in the GOM had not been completed until we concluded the study presented here. McDowell and Robillard (2013) reported that the spawning

season for this species in the SAB was March–August and that peak activity occurred in April. That finding is similar to previous results from studies in the GOM; for those studies gonads were examined macroscopically and indicated that the spawning season in the GOM lasts from February or March to November (Irwin, 1970; Crowe, 1984; Harding and Chittenden, 1987), with a peak in April (Fritzsche and Crowe[3]). Size at sexual maturity appears similar between the GOM and the SAB; Harding and Chittenden (1987) reported on the basis of macroscopic assessment that females in the northwestern GOM reach 100% maturity at an age of 12–14 months or a size of 250 mm total length (TL), and McDowell and Robillard (2013) suggested that females from the SAB reach 50% maturity at 1.1 years or 199 mm TL.

Knowledge of the reproductive biology and somatic traits of fish populations is required to assess the resiliency of populations to fishing (Nielsen and Johnson, 1983; Fulford and Hendon, 2010). To address gaps in knowledge, we describe a variety of reproductive and somatic traits, namely annual spawning season, spawning frequency, batch fecundity, and size at 50% maturity, for Southern Kingfish within the northcentral GOM that were determined by histological analysis and with standard techniques. We also quantified length at age and weight at length from analyses of nonlinear relationships. Finally, we compare these traits with traits of other recreationally and commercially important sciaenid populations in the U.S. EEZ to assess differences and similarities in life-history patterns of members of this family.

Materials and methods

Southern Kingfish were sampled from several locations in the Mississippi Sound off the coast of Mississippi from April 2008 to May 2009 (Fig. 1). We targeted with hook and line a minimum of 50 fish each month from February to October and 15 fish from November to January. Haphazardly collected samples from crab pots and otter trawls during spring and summer were also obtained. Fish were identified according to Chao (2002). Upon collection, fish were immediately placed on ice and processed in the laboratory within 24 h. Each fish was measured for TL and standard length (SL) in millimeters and weighed in grams. The left sagittal otoliths of these fish were removed, cleaned, and dried; sex was determined macroscopically when gonads were removed and weighed (0.1 g). Sex-specific gonadosomatic indices (GSIs) were calculated:

$$\text{GSI} = (GW/GFBW) \times 100, \tag{1}$$

where GW = gonad weight; and
$GFBW$ = gonad-free body weight of the fish (Greeley et al., 1986).

A small cross section from the middle of the right gonad was removed and fixed in 10% neutral buffered

[1] Armstrong, M. P., and R. G. Muller. 1996. A summary of biological information for southern kingfish (*Menticirrhus americanus*), Gulf kingfish (*M. littoralis*), and northern kingfish (*M. saxatilis*) in Florida waters. Florida Marine Research Institute (FMRI) In-house Report IHR 1996-004, 25 p. [Available from http://research.myfwc.com/publications/publication_info.asp?id=43619.]

[2] Lagarde, C. C. 1981. Environmental requirements of selected coastal finfish and shellfish of the Mississippi Sound and vicinity: Southern kingfish *Menticirrhus americanus* (Linnaeus), 5 p. [Available from Mississippi State Univ. Research Center, NSTL Station, Mississippi, 105 Mill St.; Starkville, MS 39759.]

[3] Fritzsche, R. A., and B. J. Crowe. 1981. Contributions of the life history of the southern kingfish, *Menticirrhus americanus* (Linnaeus), in Mississippi, 84 p. BMR Project No. CO-ST-79-022. [Available from Mississippi Department of Marine Resources, 1141 Bayview Ave.; Biloxi, MS 39532.]
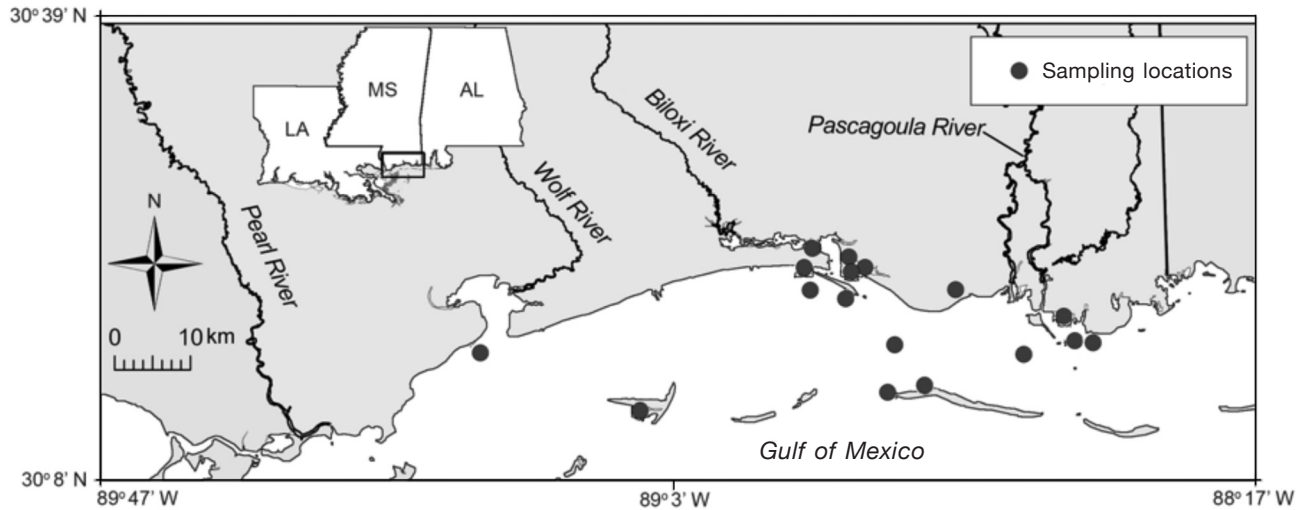
Figure 1

Map of locations where Southern Kingfish (*Menticirrhus americanus*) were sampled with hook and line and crab pots between April 2008 and May 2009 in the Mississippi Sound, Mississippi, to describe reproductive and somatic traits of this species and compare its life history with that of other sciaenids.

formalin for a minimum of 1 week for histological analysis.

Aging and aging validation of otoliths

Age estimates were determined from Southern Kingfish allocated in 10-mm-TL size classes. We randomly chose and aged up to 5 specimens per size bin; otoliths were processed as described in VanderKooy (2009). Otoliths were embedded in a resin block (Buehler Epoxicure[4] resin and hardener, Buehler, an ITW Co., Lake Bluff, IL) and sectioned at the junction of the ostium and sulcus with a saw equipped with a Norton diamond wheel (Saint-Gobain, Valley Forge, PA). These sections were sanded, mounted on labeled slides with clear Crystalbond 509 adhesive (Aremco Products, Inc., Valley Cottage, NY), and the slide was cooled and dried. The otolith sections were polished with a clear Flox-Texx mounting medium (Thermo Fisher Scientific, Inc., Waltham, MA).

Annuli were counted with a Motic BA200 microscope (Motic North America, Richmond, Canada) under transmitted light by 2 independent readers. Fully formed annuli were counted to determine the age of the fish specimen, and the outer edge margin was coded on the basis of the percentage of translucent area beyond the final opaque ring (margin codes: 1=0%, 2=33%, 3=66%, and 4=99%; [VanderKooy, 2009]). A margin code of 1 was assumed to signify the month the annulus was formed. Numbers of annuli and margin codes were compared between readers, and any discrepancies were

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[4] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

reexamined by a third reader; if agreement could not be reached, the otolith was removed from analysis. McDowell and Robillard (2013) validated that Southern Kingfish off Georgia produced a single annulus once a year.

Reproductive biology

Preserved ovaries were dehydrated, embedded in paraffin, sectioned at 4 µm, and stained with Hematoxylin 2 and Eosin Y (Thermo Fisher Scientific) for histological examination. Slides were assessed microscopically to determine ovarian phases defined by Brown-Peterson et al. (2011); the 5 reproductive phases of immature, developing, spawning capable, regressing, and regenerating, as well as the associated subphases of early developing and actively spawning, were recognized. A Southern Kingfish was defined as sexually mature once it entered the developing phase (DE) and cortical alveoli (CA) oocytes were observed.

Two quantitative approaches were used to estimate the spawning frequency of Southern Kingfish: 1) the percentage of fish in the spawning-capable phase with or without a 24-h postovulatory follicle (POF) complex (hereafter termed the POF method) and 2) the percentage of fish undergoing oocyte maturation (OM) (Hunter and Macewicz, 1985) (hereafter termed the OM method). Spawning frequency is expressed as the number of days between spawning events (see Brown-Peterson and Warren [2001] for details).

Batch fecundity (BF) was estimated for female Southern Kingfish in the actively spawning subphase. A subsample from the middle of the gonad was removed, weighed (to the nearest 0.1 g), and preserved

in modified Gilson's fluid (Bagenal, 1966) for a minimum of 3 months. Once oocytes were separated from ovarian tissue, they were suspended in water and all hydrated or OM oocytes occurring in six 1-mL aliquots were counted. Graphs of oocyte size-frequency distributions of spawning-capable and actively spawning fish were developed to identify and determine the size of OM oocytes used for counts. Batch fecundity (number of eggs) and relative batch fecundity (RBF; number of eggs per gram of ovary-free body weight [eggs g^{-1} OFBW]) were calculated by the volumetric method (Bagenal and Braum, 1971). All values for BF and RBF provided here are reported as a mean ± standard error of the mean (SE).

Comparison of sciaenid life histories

Life-history data were summarized for recreationally and commercially important sciaenid species commonly occurring in the U.S. EEZ. Species that occur infrequently in U.S. catches, have their centers of distribution outside U.S. waters, or that are important only in the aquarium trade, were excluded from the comparison. In addition, commercially or recreationally important species for which there is little life-history information were excluded from the data summary. To treat geographically separated populations of the same species individually, we recognized GOM, Pacific, and Atlantic populations within species. Data for each of these species were obtained from the literature, with the exception of Southern Kingfish, which is described in this study. We summarized 8 somatic and reproductive traits for each species: 1) maximum age (years), 2) maximum TL (millimeters), 3) spawning-season duration (months), 4) spawning frequency (days), 5) RBF (eggs g^{-1} OFBW), 6) age at maturity (years), 7) TL at maturity (millimeters), and 8) the parameter b (morphology index: exponent of weight at length from the power function) in the 2-parameter power function used to describe weight at length ($W = a TL^b$).

Data analyses

Somatic patterns of Southern Kingfish were quantified with linear and nonlinear relationships. The mean TL at 50% maturity (TL_{50}) was estimated with a 2-parameter logistic model:

$$M_{TL} = \frac{1}{1 + e^{-r(TL - TL_{50})}}, \qquad (2)$$

where female maturity was coded binomially as immature (0) or mature (1).

The relationship between sex-specific SL and TL was estimated with a linear model:

$$SL = \beta_0 + \beta_1 \times TL. \qquad (3)$$

We used a 2-parameter von Bertalanffy growth function (VBGF) to describe length at age:

$$TL_t = TL_\infty (1 - e^{-kt}), \qquad (4)$$

where TL_t = TL of a fish with age t:

The VBGF model parameters were TL_∞ (the mean hypothetical maximum TL achieved by an individual, in millimeters) and the growth coefficient k (the rate of growth, per year). We estimated longevity as the age (in years) taken to reach 95% and 99% of predicted TL_∞ (Fabens, 1965; Ricker, 1979) and used a power function to determine mean weight at length. The 95% confidence intervals (CI) of the mean model parameters for the VBGF, power, and logistic functions were determined by using the confint algorithm distributed in the stats package in the base version of the program R (vers. 2.15.1; R Core Team, 2012).

The GSI values were arcsine square-root transformed before analysis and were tested for normality (Kolmogorov-Smirnov one-sample test) and homogeneity of variance (Levene's test). A one-way analysis of variance (ANOVA) tested for GSI differences among months by sex. If a significant F-value was observed, monthly values were separated with a Sidak pairwise test; if the data were heterogeneous, a Games-Howell (GH) test was used (Field, 2005). Differences in spawning frequency among seasons (early, mid, and late) were tested with a chi-square test. Linear regressions of $\log_{10}$-transformed data were used to determine if there were relationships between either BF or RBF as the dependent variable and TL, OFBW, and age as the independent variables. The SPSS program (vers. 20.0; IBM Corp., Armonk, NY) was used, and the significance level was $P < 0.05$.

Principal components analysis (PCA) was used to compare and describe the multivariate somatic and reproductive traits of 17 geographic populations (14 species) in the family Sciaenidae. We limited our PCA to those populations that had available data for 5 somatic and reproductive traits. Somatic traits included the maximum TL and the parameter b; reproductive traits included duration of spawning season, RBF, and age at maturity. In cases where more than one value was reported for a trait, the median value was used for the PCA. The PCA was performed by eigenvalue decomposition of the correlation matrix with varimax rotation to maximally resolve loadings, and only eigenvalues >1.0 were used. We considered any variable that loaded on a component at $|\geq 0.60|$ to make a significant contribution to interpretation of that component (Hair et al., 1984). The SPSS program was used, and the significance level was $P < 0.05$.

Results

Somatic characteristics

From April 2008 to May 2009, 519 Southern Kingfish (434 females, 85 males) were sampled; no fish were collected in January 2009. Of these fish, 508 were collect-

Table 1

Sample size (*n*), mean total length (TL, in millimeters) and minimum and maximum TL values by month and sex for Southern Kingfish (*Menticirrhus americanus*) collected in Mississippi Sound, Mississippi, from April 2008 to May 2009.

Date	Female				Male			
	n	Mean TL	Min TL	Max TL	*n*	Mean TL	Min TL	Max TL
April 2008	45	232	192	267	3	234	227	244
May 2008	3	270	231	303	–	–	–	–
June 2008	45	217	164	312	29	193	173	224
July 2008	42	243	163	348	10	226	180	256
August 2008	33	254	219	331	7	231	212	267
September 2008	51	252	191	328	3	233	226	242
October 2008	49	238	182	341	6	222	215	240
November 2008	16	258	205	307	2	212	203	220
December 2008	3	266	246	278	2	233	221	244
February 2009	45	239	181	283	10	217	198	263
March 2009	49	229	135	279	6	210	171	244
April 2009	11	246	148	280	2	199	198	200
May 2009	42	232	184	300	5	207	191	224
Overall	434	–	135	348	85	–	171	267

ed with hook and line, 7 were collected in otter trawls, and 4 were collected from crab pots. All haphazardly sampled specimens were within the normal size distribution (trawls, 187–300 mm TL; crab pots, 263–280 mm TL). Sizes of females were recorded in ranges of 135–348 mm TL and 24.8–530.2 g; males fell in size ranges of 171–267 mm TL and 49.4–213.4 g (Table 1; Fig. 2, A and B). There was a significant linear relationship between TL and SL for both sexes (Table 2; males: $P<0.0001$, coefficient of multiple determination [R^2]=0.98; females: $P<0.0001$, R^2=0.96).

Comparison of the mean values and confidence intervals derived in the VBGF analysis indicated that males reach a significantly smaller asymptotic TL (α=0.05) and grow faster than females (Fig. 2, A and B; Table 2). Females at all ages had a greater mean length than that of males (Fig. 2C). The estimated longevity, calculated with the mean VBGF parameters, was 3.1–4.3 years for males and 3.6–5.1 years for females (Table 2). Significant differences in both *a* and *b* parameters were observed by comparing mean and 95% CI values in the weight-at-length relationship (parameter *a* was the coefficient of the power function). Females had a significantly greater mean value of the power function exponent (parameter *b*) than had males: 3.26 versus 2.88 (α=0.05; Table 2).
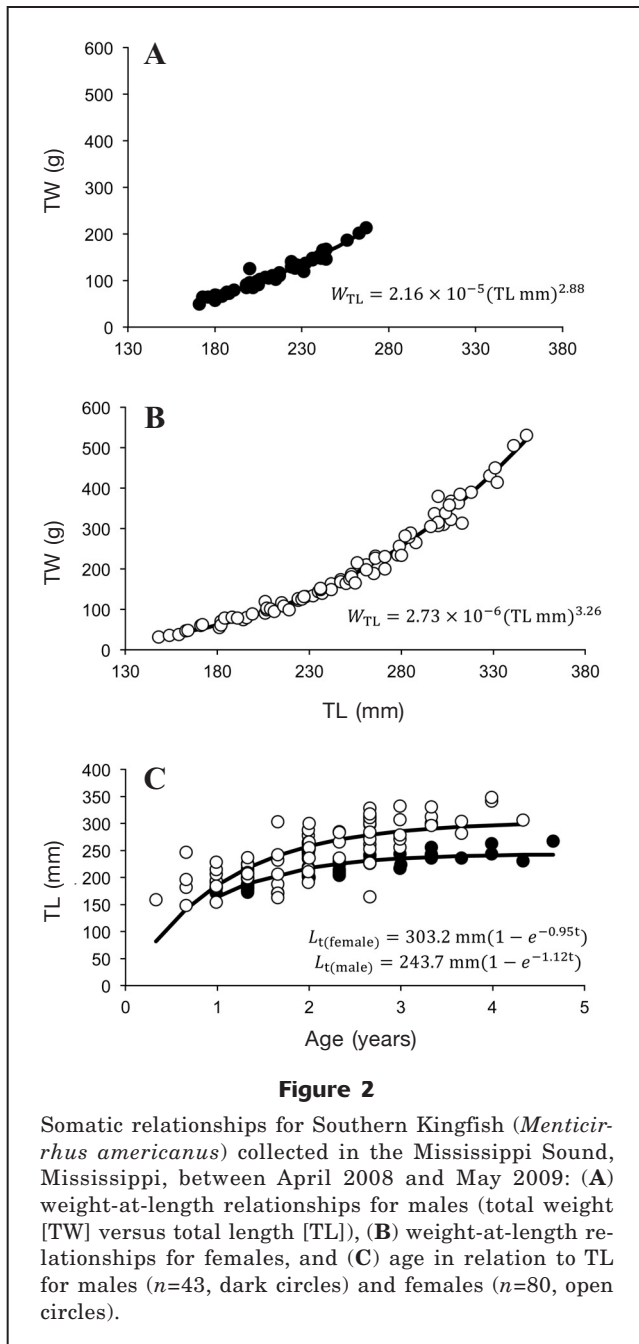
Age determined from otoliths

Alternating opaque and translucent annuli were distinctive in the prepared cross sections of Southern Kingfish otoliths (Fig. 3A). Marginal increment analy-

sis showed that Southern Kingfish in the GOM form opaque annuli during April and May, on the basis of the presence of fish with a margin code of 1 (0% translucence above the opaque annulus; Fig. 3B). A single fish had a margin code of 1 in June, although 2 was the dominant margin code in June and July (78% and 73% of fish, respectively). Fish with a margin code of 2 showed active accretion of the otolith beyond the formation of the opaque annulus. Margin codes 3 and 4 were most common from August to March; margin code 4 was dominant in February and March, just before the deposition of the opaque annulus (Fig. 3B).

There were 5 age classes (age 0–4) observed in the sampled mature population (*n*=123) of Southern Kingfish in the northcentral GOM. Fish of age 1 and 2 were the largest groups, accounting for 39% and 33% of the total, respectively. Because of the sampling technique used, young-of-the-year (age-0) fish composed only 12%, and fish of age 3 and 4 represented 13% and 3% of the sample, respectively.

Reproductive characteristics

Of the 519 Southern Kingfish collected, ovary samples from 397 females were processed for histological analysis. The smallest female observed to reach sexual maturity was 163 mm TL and age 1. Only 3.5% of the 397 females histologically examined were found to be immature. Estimated size at L_{50} was 171 mm TL (Fig. 4; R^2=0.71, *n*=396). All females >211 mm TL were sexually mature and were age 1 or older.

Figure 2

Somatic relationships for Southern Kingfish (*Menticirrhus americanus*) collected in the Mississippi Sound, Mississippi, between April 2008 and May 2009: (**A**) weight-at-length relationships for males (total weight [TW] versus total length [TL]), (**B**) weight-at-length relationships for females, and (**C**) age in relation to TL for males (n=43, dark circles) and females (n=80, open circles).

$P<0.0001$), peaking in April and reaching the lowest values in November (Sidak; $P<0.05$).

Histological analysis confirmed the Southern Kingfish spawning season that had been indicated by GSI value in our analysis. The majority of the females were in the early developing subphase in February; this percentage decreased in March as fish moved into the developing phase (Table 3). Females were first observed in the spawning capable phase (Fig. 5B) in March, although no POFs were seen in March. From April to August, ≥78% of captured females were in the spawning-capable phase; this percentage decreased to 59% by September (Table 3). Females in the actively spawning subphase were found from April to September (Table 3). Although some females were found in the spawning-capable phase in October (13%), the majority of fish were in the regressing and regenerating phases, signaling the end of the reproductive season. By November, all females were reproductively inactive (Table 3). Therefore, on the basis of histological observations, the spawning season for Southern Kingfish in the northcentral GOM appears to be April–September. Furthermore, the asynchronous oocyte development observed in females in the spawning-capable phase (Figs. 5B and 6) indicates that Southern Kingfish is a batch-spawning species in the northcentral GOM.

Seasonal spawning frequencies were estimated with both the POF and OM calculation methods, and they were calculated only for months when actively spawning females were observed (Table 4). Results were similar between methods for the early and mid-season spawning frequencies but differed during the late season. There was a significant difference seasonally for frequencies calculated with the POF method (χ^2=17.50, df=2, $P<0.0001$) but not for values estimated with the OM method (χ^2=3.251, df=2, $P>0.05$). Both methods revealed a spawning frequency of 11.3 days between spawns for the early season (April–May). During the mid-season (June–July), spawning frequency ranged from 3.5 to 5.8 days between spawnings depending on the method. Spawning frequency in the late season (August–September) was much greater for the OM method (5.4 days) compared with the POF method (19.7 days). The mean annual spawning frequency was calculated for both methods at 6.9 days between spawnings (Table 4). Therefore, over the course of the entire spawning season (April–September), Southern Kingfish spawn on average once every 7 days and an individual has the potential to spawn 26 times.

Batch fecundity estimates were compared for 11 females that were in the actively spawning subphase. A distinct group of oocytes >350 μm was observed in actively spawning fish; therefore, oocytes >350 μm were considered to be undergoing OM (Fig. 6) and were counted for fecundity analysis. Overall BF ranged from 17,338 to 80,495 eggs and had a mean of 35,571 eggs (SE 6405) (Table 5). There were no significant relationships between $\log_{10}$ BF and $\log_{10}$ TL (R^2=0.199, $F_{1,9}$=2.23, P=0.169) or $\log_{10}$ BF and $\log_{10}$ OFBW

Female GSI increased from February to April, remained relatively high from May to August, and decreased thereafter (Fig. 5A). Female GSI among months was significantly different (ANOVA: $F_{10,\ 423}$=32.49; $P<0.0001$) with values for March–September significantly higher than those for all other months (GH, $P<0.05$), indicating Southern Kingfish may spawn in the northcentral GOM from March to September. Male GSI mirrored that of females (Fig. 5A) and was significantly different among months (ANOVA: $F_{10,\ 74}$=7.65;
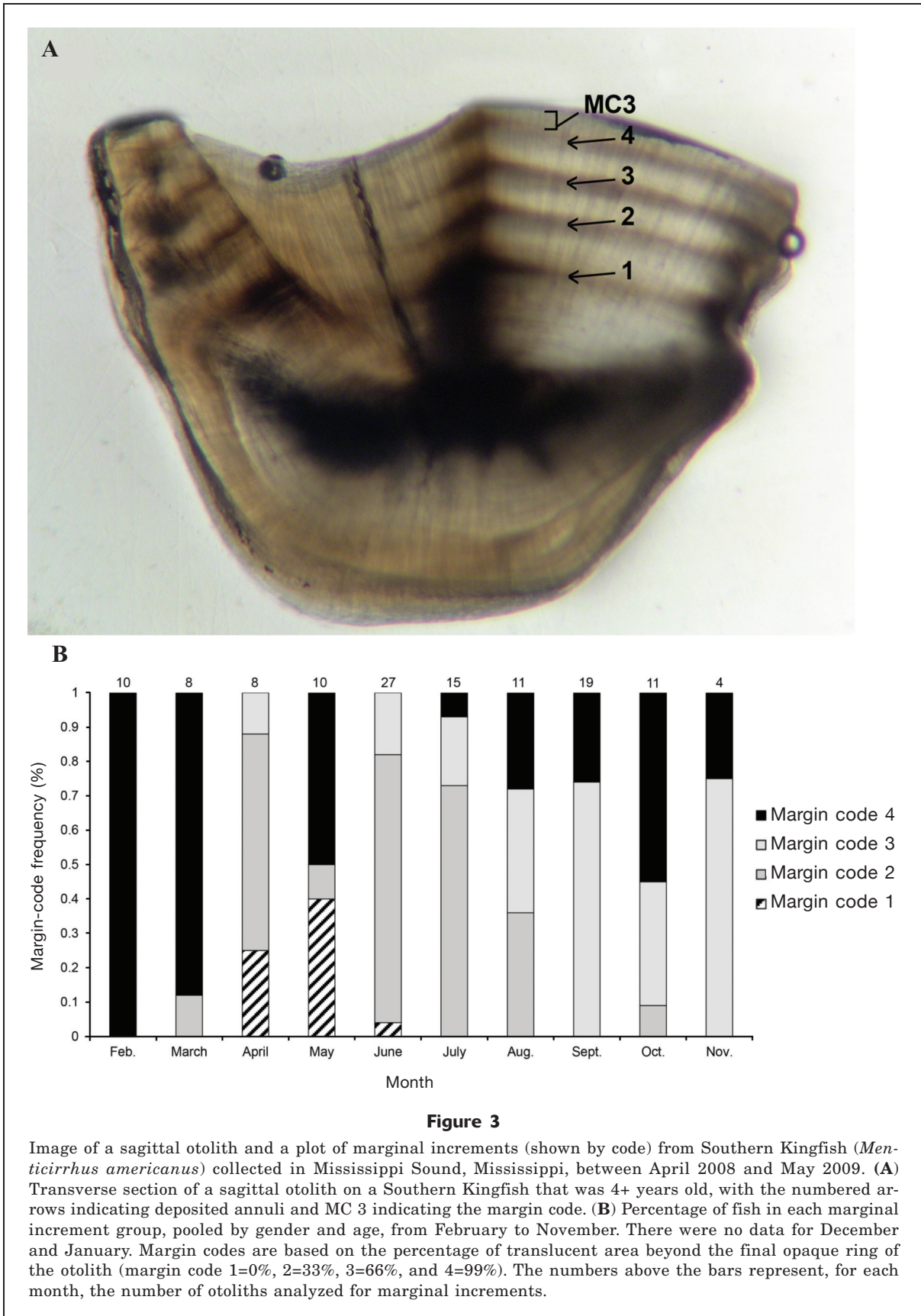
Table 2

Summary of equations and related statistics used in this study for analyses of Southern Kingfish (*Menticirrhus americanus*) collected in Mississippi Sound, Mississippi, between April 2008 and May 2009. W=somatic wet weight (in grams), TL=total length (in millimeters), SL=standard length (in millimeters), coefficient of multiple determination (R^2), coefficient of correlation (r), CI=confidence intervals, y=year, β_1=slope of simple linear regression, β_0=y-intercept of simple linear regression, k=is a growth rate constant (y^{-1}), TL_∞=is the mean maximum TL (mm), TL_t=TL at time t (mm), t=time, r=instantaneous rate of increase (mm^{-1}), a= coefficient of the power function, b= exponent of the power function, TL_{50}= total length at 50% maturity, $\rho_{95\%}$ and $\rho_{99\%}$= the age (y) taken to reach 95% and 99% of predicted TL_∞.
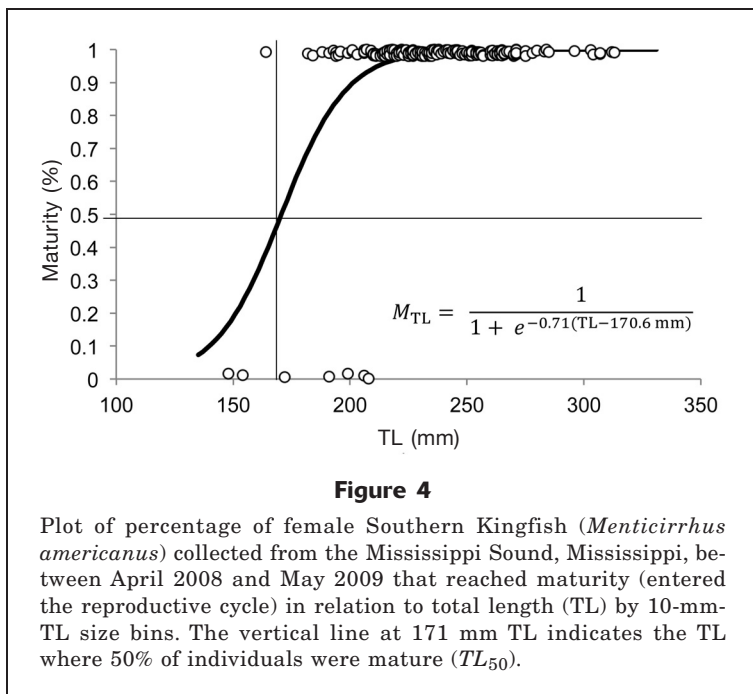
Analysis	Model name (model formulation)	Sex	n	R^2	P	Parameter	Estimated mean parameter value (minimum to maximum 95% CI)
SL vs. TL	Linear $SL = \beta_0 + \beta_1 \times TL$	Female	434	0.96	<0.001	β_0 β_1	−6.26 (−10.43 to −2.08) 0.85 (0.83 to 0.87)
		Male	85	0.98	<0.001	β_0 β_1	−8.26 (−13.45 to −3.08) 0.86 (0.84 to 0.89)
Length-at-age	2-parameter von Bertalanffy growth function $TL_t = TL_\infty(1 - e^{-kt})$	Female	89	0.57	–	k	0.95 y^{-1} (0.76 to 1.16 y^{-1})
						TL_∞	303.2 mm (284.7 to 328.6 mm)
		Male	43	0.75	–	k TL_∞	1.12 y^{-1} (0.99 to 1.26 y^{-1}) 243.7 mm (235.6 to 252.7 mm)
Weight at length	Power function $W = aTL^b$	Female	80	0.98	–	a	2.73×10^{-6} (1.42×10^{-6} to 4.78×10^{-6})
						b	3.26 (3.16 to 3.37)
		Male	43	0.96	–	a	2.16×10^{-5} (7.14×10^{-6} to 5.48×10^{-5})
						b	2.88 (2.71 to 3.09)
Longevity	95% and 99% of predicted L_∞	Female	–	–	–	$\beta_{95\%}$ $\beta_{99\%}$	3.6 y 5.1 y
		Male	–	–	–	$\beta_{95\%}$ $\beta_{99\%}$	3.1 y 4.3 y
Maturity	2-parameter logistic function $M_{TL} = (1 + e^{-r(TL - TL_{50})})^{-1}$	Female	396	0.37	–	r TL_{50}	0.71 y^{-1} (0.06 to 0.09 y^{-1}) 170.6 mm (166.8 to 176.6 mm)

Table 3

Percentages of spawning female Southern Kingfish (*Menticirrhus americanus*) by month and spawning phase on the basis of histological analysis. Samples were collected in Mississippi Sound, Mississippi, between April 2008 and May 2009. Actively spawning is a subphase of the spawning-capable phase.

Spawning phases	Month n	Feb. 44	Mar. 49	Apr. 44	May 45	Jun. 40	July 41	Aug. 33	Sep. 49	Oct. 37	Nov. 13	Dec. 2
Immature		2	6	2	13	2	5	0	0	0	0	0
Developing		2	31	0	0	2	0	0	0	3	0	0
Early developing		64	24	5	2	8	0	0	0	0	0	0
Spawning-capable		0	39	86	76	63	80	76	47	13	0	0
Actively spawning		0	0	7	9	15	15	15	12	0	0	0
Regressing		0	0	0	0	10	0	0	8	35	8	0
Regenerating		32	0	0	0	0	0	9	33	49	92	100

Figure 3

Image of a sagittal otolith and a plot of marginal increments (shown by code) from Southern Kingfish (*Menticirrhus americanus*) collected in Mississippi Sound, Mississippi, between April 2008 and May 2009. (**A**) Transverse section of a sagittal otolith on a Southern Kingfish that was 4+ years old, with the numbered arrows indicating deposited annuli and MC 3 indicating the margin code. (**B**) Percentage of fish in each marginal increment group, pooled by gender and age, from February to November. There were no data for December and January. Margin codes are based on the percentage of translucent area beyond the final opaque ring of the otolith (margin code 1=0%, 2=33%, 3=66%, and 4=99%). The numbers above the bars represent, for each month, the number of otoliths analyzed for marginal increments.

Figure 4

Plot of percentage of female Southern Kingfish (*Menticirrhus americanus*) collected from the Mississippi Sound, Mississippi, between April 2008 and May 2009 that reached maturity (entered the reproductive cycle) in relation to total length (TL) by 10-mm-TL size bins. The vertical line at 171 mm TL indicates the TL where 50% of individuals were mature (TL_{50}).

$$M_{TL} = \frac{1}{1 + e^{-0.71(TL-170.6 \, mm)}}$$

(R^2=0.164, $F_{1, 9}$=1.77, P=0.216). The 11 specimens used in the fecundity calculations were collected in May, July, August, and September, and the highest mean BF occurred in August at 38,722 eggs (SE 20,288) and the lowest mean BF, in September at 33,730 eggs (SE 12,544). There were only 2 age classes represented in the fecundity analysis: age-1 (*n*=4) and age-2 (*n*=7) fish (Table 5). Mean BF was slightly higher in age-2 fish at 36,622 eggs (SE 6122) than in age-1 fish at 33,730 eggs (SE 15,591); however, there was no significant relationship between log_{10} BF and log_{10} age (R^2=0.015, $F_{1, 9}$=0.136, P=0.721).

Relative batch fecundity had a range of 94.4–509.5 eggs g^{-1} OFBW and a mean of 213.1 eggs g^{-1} OFBW (SE 35.7) (Table 5). Like the BF results, results for RBF had its highest mean in August at 259.6 eggs g^{-1} OFBW (SE 124.9) and lowest mean in September at 168.1 eggs g^{-1} OFBW (SE 70.3). Unlike the BF results, results for mean RBF were lower in age-2 fish, with 200.2 eggs g^{-1} OFBW (SE 29.4), than in age-1 fish, with 235.7 eggs g^{-1} OFBW (SE 91.5). Potential annual fecundity for Southern Kingfish in the northcentral GOM indicates that a female with a somatic wet weight of 176 g could potentially spawn 924,846 eggs over the course of the spawning season.

Sciaenidae life-history traits: a comparative analysis

Wide variation was observed in the somatic and reproductive traits examined for the 21 sciaenid populations that were analyzed in this study (Appendix table). For instance, Silver Seatrout (*Cynoscion nothus*), a GOM species, has the lowest reported maximum age (1.5 years) of the 21 species, but Black Drum (*Pogonias cromis*), another GOM species, has the oldest reported maximum age (43 years). Duration of spawning season ranged from 2 months (Black Drum) to 7–10 months for White Croaker (*Genyonemus lineatus*), a Pacific species. Size at maturity varied from 110–120 mm TL in Silver Perch (*Bairdiella chrysoura*), a GOM species, to 900 mm TL for Atlantic populations of the Red Drum (*Sciaenops ocellatus*). Life-history traits least frequently reported for sciaenid species include RBF and spawning frequency (Appendix table). Of the 11 species or populations with available spawning-frequency data, Queenfish (*Seriphus politus*) has the longest interspawning interval of 7.4 days and Silver Perch has the shortest interval of 1.3–1.6 days.

The PCA of the 5 somatic and reproductive traits produced 2 meaningful components that accounted for 68.1% of the total variation of the original data set. The first principal component (PC 1) accounted for 43.1%, whereas the second principal component (PC 2) accounted for 25.0%. Maximum TL and age at maturity both positively loaded on PC 1, but RBF loaded negatively on PC 1 (Table 6). In contrast, duration of spawning season and parameter *b* loaded positively on PC 2 (Table 6). We interpret PC 1 as a size-related component of life history, and PC 2 represents spawning season dynamics. Overall, the PCA indicated 3 general trends in sciaenid life history: 1) fishes that reach a larger maximum TL and older age at maturity tend to have lower RBF, 2) a higher RBF is associated with a shorter spawning-season duration, and 3) a longer spawning-season duration is associated with fishes that have higher *b* values.

Five groups of sciaenid populations can be discerned in the PCA biplot (Fig. 7). Group A, consisting of fishes with high maximum TL, greater age at maturity, and low RBF, is composed of GOM species Red Drum and Black Drum. Group B consists of fishes with longer spawning seasons, greater *b* values, low RBF, smaller maximum TL, and lower age at maturity and is represented by Sand Seatrout (*Cynoscion arenarius*), Southern Kingfish, White Croaker, and Queenfish, a mixture of species from all 3 regions, the GOM as well as the Atlantic and Pacific. Group C, made up of fishes with higher RBF, shorter spawning season, young age at maturity, small maximum TL, and low *b* values, is represented by 2 GOM species: Spot (*Leiostomus xanthurus*) and Silver Perch. Group D consists of fishes with more intermediate traits, such as small maximum TL, low age at maturity, and moderate spawning season, *b* values, and RBF. A species each from the Atlantic and GOM represent group D: Atlantic Croaker (*Micropogonias undulatus*) and Silver Seatrout. Finally, group E also is an intermediate group with characteristics of
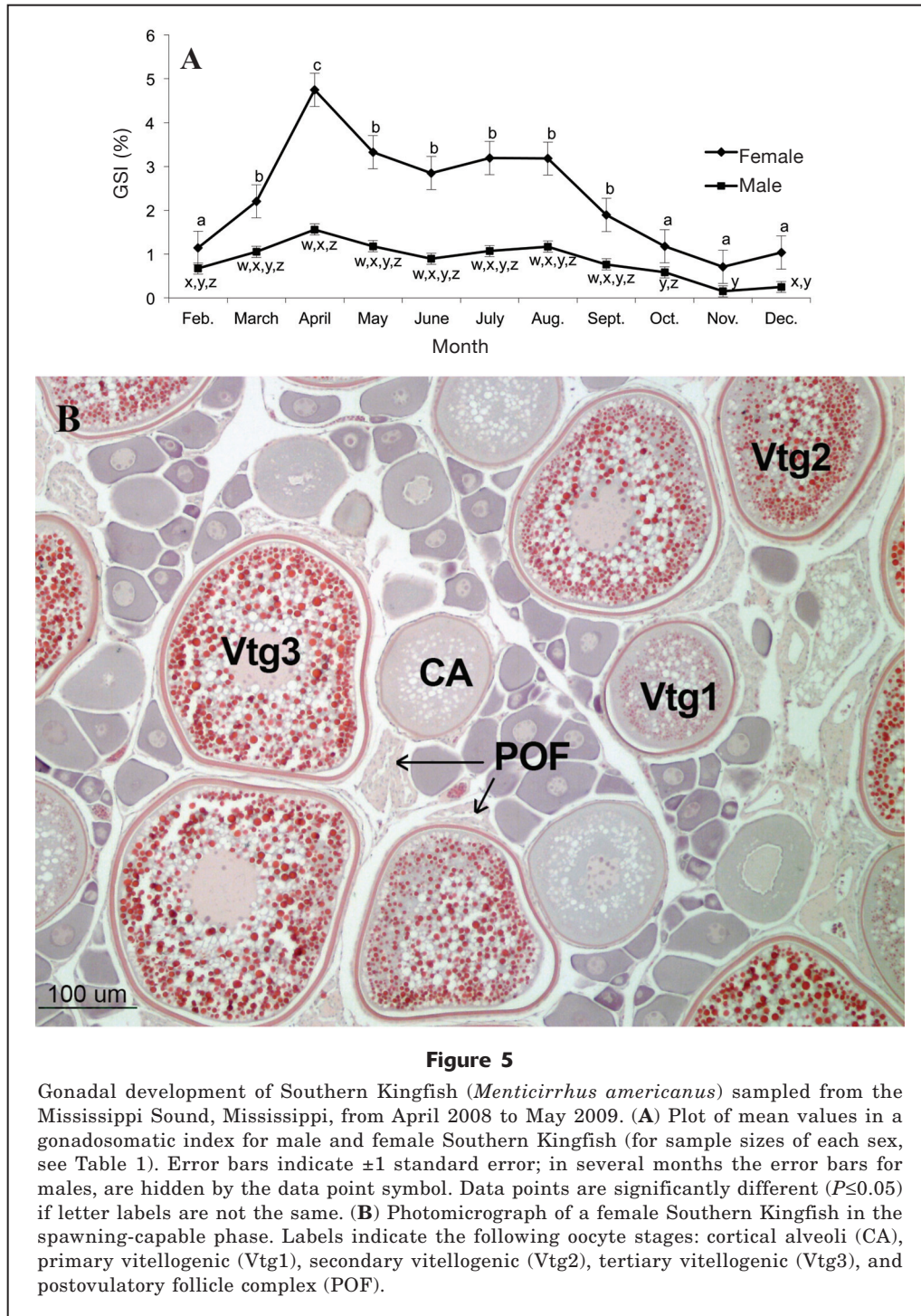
Figure 5

Gonadal development of Southern Kingfish (*Menticirrhus americanus*) sampled from the Mississippi Sound, Mississippi, from April 2008 to May 2009. (**A**) Plot of mean values in a gonadosomatic index for male and female Southern Kingfish (for sample sizes of each sex, see Table 1). Error bars indicate ±1 standard error; in several months the error bars for males, are hidden by the data point symbol. Data points are significantly different ($P \leq 0.05$) if letter labels are not the same. (**B**) Photomicrograph of a female Southern Kingfish in the spawning-capable phase. Labels indicate the following oocyte stages: cortical alveoli (CA), primary vitellogenic (Vtg1), secondary vitellogenic (Vtg2), tertiary vitellogenic (Vtg3), and postovulatory follicle complex (POF).

moderate maximum TL, age, RBF, duration of spawning season, and *b* values. Group E comprises fishes from all 3 regions: Spotted Seatrout (*Cynoscion nebulosus*) from Atlantic and GOM populations, as well as Weakfish (*Cynoscion regalis*), Spotfin Croaker (*Roncador stearnsii*), and Yellowfin Croaker (*Umbrina roncador*).

Discussion

In this article, we identify and address gaps in the understanding of the life history of the recreationally and commercially important Southern Kingfish in the northcentral GOM. We report that Southern Kingfish

Table 4

Seasonal spawning frequency for Southern Kingfish (*Menticirrhus americanus*) in the northcentral Gulf of Mexico determined with 2 histological methods. The postovulatory follicle (POF) method is based on the presence of POF ≤24 h and the oocyte maturation (OM) method is based on the presence of oocytes in OM. Only females in the spawning capable phase (including the actively spawning subphase) were used in this analysis. Samples were collected from Mississippi Sound, Mississippi, between April 2008 and May 2009.

Season	n	POF spawning frequency (days)	OM spawning frequency (days)
Early (April–May)	79	11.29	11.29
Mid (June–July)	70	3.50	5.83
Late (Aug.–Sept.)	59	19.67	5.36
Total (April–Sept.)	208	6.93	6.93

tions in estuaries, the surf zone, or the shallow inshore waters could resolve whether there are 2 discrete spawning periods, as they have suggested, or 1 spawning period with 2 periods of recruitment.

Although GSI values are typically good indicators of spawning preparedness, histological analysis can refine and more precisely delineate the spawning season and has not been previously performed for Southern Kingfish from the GOM. The spawning season estimated through our histological analysis matched our GSI results; spawning is initiated in April and ends in September. Additionally, there were fish in the spawning-capable phase in both March and October, although no females were in the actively spawning subphase during these months. Our estimate of the Southern Kingfish spawning period is supported by Anderson et al. (2012), who studied daily growth rings in otoliths from juveniles in the northcentral GOM and estimated birth dates with back calculation. Although there were fish in that study with

has a 6-month spawning period that occurs from spring to summer and that an individual female spawns, on average, 213.1 eggs g^{-1} OFBW once per week. Females reach sexual maturity at a relatively small size (171 mm TL) and young age (1+ years). We report significant differences in sex-specific length at age and weight at length. Finally, we document how the life-history traits of this species are part of the multivariate continuum of sciaenid stocks in the coastal waters of the continental United States.
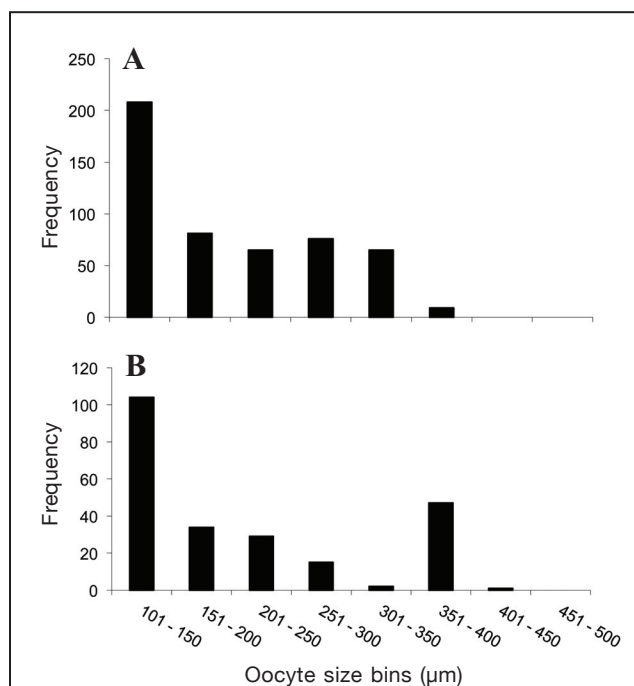
Our analysis of the reproductive traits of the Southern Kingfish provided the timing of spawning through the use of both GSI and histological analysis, and we identified a single, extended spawning period. The spawning season for Southern Kingfish in the northcentral GOM begins in late March and ends in September, with peaks in male (1.56%) and female (4.75%) GSI values in April. Other investigators have previously reported similar spawning seasons for Southern Kingfish in both the Atlantic and GOM on the basis of macroscopic inspection of the ovary and GSI values (Hildebrand and Cable, 1934; Bearden, 1963; Lagarde[2]; Smith and Wenner, 1985; McDowell and Robillard, 2013). An extended spawning season (≥3 months) is characteristic of most sciaenid species (Appendix). Our analysis of this reproductive trait places Southern Kingfish in group B (see Fig. 7), a group partially characterized by having the longest spawning season.

Our finding of the existence of a single spawning season is in contrast to results from Harding and Chittenden (1987), who found on the basis of male and female GSI and macroscopic classification of maturity that the spawning period in the northwestern GOM occurred from February or March to November and comprised 2 primary, discrete spawning periods (spring and fall). However, the Harding and Chittenden (1987) collections were from the deeper part of the bathymetric range of Southern Kingfish; more thorough collec-

Figure 6

Oocyte size frequency distribution for Southern Kingfish (*Menticirrhus americanus*) collected from the Mississippi Sound, Mississippi, between April 2008 and May 2009 and found to be in the (**A**) spawning-capable phase or (**B**) actively spawning subphase.

Table 5

Mean batch fecundity (number of eggs) and relative batch fecundity (number of eggs per gram of ovary-free body weight) by month and age class for Southern King-fish (*Menticirrhus americanus*) collected between April 2008 and May 2009 from the northcentral Gulf of Mexico (Mississippi Sound, Mississippi). Standard errors of the mean (SE) are provided in parentheses.

Month or age	n	Mean batch fecundity (SE)	Mean relative batch fecundity (SE)
May	2	33,944 (2408)	228.0 (25.1)
July	3	35,150 (12,213)	201.6 (18.9)
August	3	38,722 (20,888)	259.6 (124.9)
September	3	33,924 (12,544)	168.1 (70.3)
Age 1	4	33,730 (15,591)	235.7 (91.5)
Age 2	7	36,622 (6122)	200.2 (29.4)
Overall	11	35,571 (6405)	213.1 (35.7)

estimated birth dates in late March (n=5), the greatest frequencies occurred between June and August, and this period marks the plateau in GSI values and the highest percentages of actively spawning fish noted from histological analysis. This evidence indicates that the notion of 2 discrete spawning periods within the season does not apply to this population. Furthermore, our data are in close agreement with recent histological analyses of Southern Kingfish from the SAB, where this species also has a single spawning period. McDowell and Robilland (2013) found spawning fish in Georgia estuaries from March to July, although spawning-capable females were seen also in August and September.

Fecundity data provide information that will aid in

Table 6

Summary of loadings from principal components analysis (PCA) of the 5 somatic and reproductive variables onto the 2 most meaningful principal components (PC 1 and PC 2). Loadings represent Pearson's correlations of original metrics to each component. Only correlation values |≥0.60| (shown in bold) are considered useful for naming components (Hair et al., 1984). Maximum total length is presented in millimeters, duration of spawning season is shown in months, relative batch fecundity is reported in number of eggs per gram of ovary-free body weight and age at maturity is presented in years; b=slope of length-weight power function.

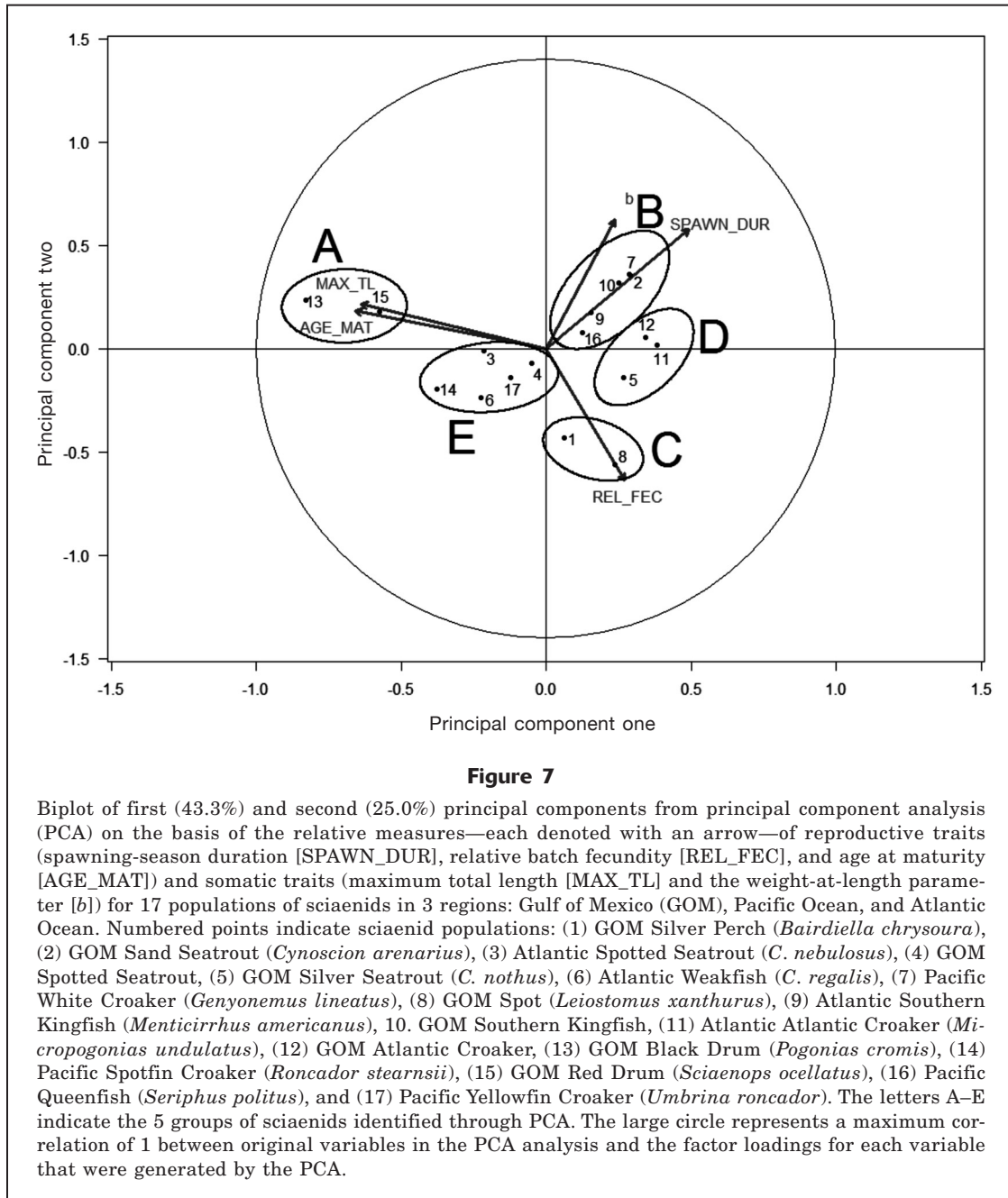| Variable	PC 1	PC 2
Maximum total length	**0.853**	−0.210
Spawning-season duration	−0.297	**0.830**
Relative batch fecundity	**−0.626**	−0.396
Age at maturity	**0.861**	−0.252
b	0.023	**0.708**

the determination of the spawning potential of Southern Kingfish at different lengths and ages; however, fecundity measurements are poorly understood for the Southern Kingfish across its range. Previously reported estimates for 20 females in the northcentral GOM (Fritzsche and Crowe[3]) were a mean BF of 105,359 eggs (range: 46,024–332,229 eggs) and a mean RBF of 527 eggs g^{-1} OFBW, but these 2 estimates are based on all oocytes >300 µm. Our data show that vitellogenic oocytes between 300 and 350 µm do not undergo OM and, therefore, represent several potential batches. Batch fecundity estimates in our study were lower than those found by Fritzsche and Crowe[3] because only hydrated oocytes or those oocytes undergoing OM were used. Militelli et al. (2013) reported RBF estimates for 8 Southern Kingfish from Argentina as 217 eggs g^{-1} OFBW (SE 70)—a finding that is similar to our results of 231 eggs g^{-1} OFBW (SE 36) for fish in the northcentral GOM. McDowell and Robillard (2013) did not directly report RBF data for Southern Kingfish from Georgia, but we calculated RBF to be 308.6 eggs g^{-1} total weight (SE 27.6) on the basis of information in their manuscript.

The lack of a significant relationship in our data between BF or RBF and TL, OFBW, or age is unusual, but it may be linked to our small sample size and the potential for significant variation in fecundity among individuals within a protracted spawning season (Lowerre-Barbieri et al., 2009). McDowell and Robillard (2013) had a more robust sample size of 36 fish and found a significant relationship between batch fecundity and both length and weight. Therefore, our fecundity estimates should be viewed with caution, despite their similarity to fecundity estimates of the Argentinean stock. Overall, Southern Kingfish exhibit some of the lowest reported RBF values for sciaenids (Appendix), a trait shared with the other members of group B in the PCA (see Fig. 7): Sand Seatrout, White Croaker, and Queenfish.

Figure 7

Biplot of first (43.3%) and second (25.0%) principal components from principal component analysis (PCA) on the basis of the relative measures—each denoted with an arrow—of reproductive traits (spawning-season duration [SPAWN_DUR], relative batch fecundity [REL_FEC], and age at maturity [AGE_MAT]) and somatic traits (maximum total length [MAX_TL] and the weight-at-length parameter [*b*]) for 17 populations of sciaenids in 3 regions: Gulf of Mexico (GOM), Pacific Ocean, and Atlantic Ocean. Numbered points indicate sciaenid populations: (1) GOM Silver Perch (*Bairdiella chrysoura*), (2) GOM Sand Seatrout (*Cynoscion arenarius*), (3) Atlantic Spotted Seatrout (*C. nebulosus*), (4) GOM Spotted Seatrout, (5) GOM Silver Seatrout (*C. nothus*), (6) Atlantic Weakfish (*C. regalis*), (7) Pacific White Croaker (*Genyonemus lineatus*), (8) GOM Spot (*Leiostomus xanthurus*), (9) Atlantic Southern Kingfish (*Menticirrhus americanus*), 10. GOM Southern Kingfish, (11) Atlantic Atlantic Croaker (*Micropogonias undulatus*), (12) GOM Atlantic Croaker, (13) GOM Black Drum (*Pogonias cromis*), (14) Pacific Spotfin Croaker (*Roncador stearnsii*), (15) GOM Red Drum (*Sciaenops ocellatus*), (16) Pacific Queenfish (*Seriphus politus*), and (17) Pacific Yellowfin Croaker (*Umbrina roncador*). The letters A–E indicate the 5 groups of sciaenids identified through PCA. The large circle represents a maximum correlation of 1 between original variables in the PCA analysis and the factor loadings for each variable that were generated by the PCA.

Spawning frequency for batch-spawning species like Southern Kingfish, when combined with batch fecundity, provides an estimate of the total annual reproductive output of a species. Histological confirmation of multiple spawnings per season for populations of Southern Kingfish in Brazil and the SAB have been reported recently on the basis of the appearance of POFs and surrounding oocytes in multiple stages of development (Haluch et al., 2011; McDowell and Robillard, 2013). In our study, the seasonal spawning frequency was found to be about 7 days between spawnings with a peak of 3–6 days (depending on method, POF or OM) during June and July in the northcentral GOM. This interspawning interval is one of the longest ones reported among the Sciaenidae (see Appendix) and contrasts with that of 2–4 days between spawnings for the SAB population of Southern Kingfish (McDowell and Robillard, 2013). However, spawning-frequency data are based on a 4-month spawning season in Georgia and a 6-month season in the GOM—a difference that may account for some of this variation.

Unfortunately, spawning-frequency data are available for only 11 of the 24 economically important sciaenid species or populations and, for that reason, were not included in the PCA of reproductive and somatic traits. Therefore, the importance of spawning frequency to the reproductive and somatic relationships between Southern Kingfish and other sciaenids is unknown.

The OM method appeared to be a reliable indicator of spawning frequency of Southern Kingfish in the GOM. Similarly, McDowell and Robillard (2013) used the OM method (specifically, presence of hydrated oocytes) to determine spawning frequency of Southern Kingfish from the SAB, although they did not present seasonal differences in spawning frequency. In our study, the OM method indicated that no significant difference existed between seasons as was observed with the POF method. The interspawning interval at the end of the season was longer when calculated by the POF method than when estimated with the OM method—a result that was likely due to a sampling bias. Fish that had finished spawning for the year may have moved out of the sample areas, whereas females that were still preparing to spawn remained in those areas. Therefore, fish that contained oocytes in the OM stage may have been more vulnerable to capture than fish with POFs. Similar differences in spawning frequency between methods were noted in the late season of Silver Perch (Grammer et al., 2009), where the OM method revealed an estimated 1.6 days between spawnings and the POF method indicated an estimated 16 days between spawnings. Although Grammer et al. (2009) stated their results may have been a function of low sample size (n=16), our study had a larger sample size (n=59) that should not have been a contributing factor to the large difference observed. Interestingly, on the basis of percentage of spawning fish captured (OM method), spawning frequency of Southern Kingfish from Georgia also was highest at the beginning of the reproductive season (March and April; McDowell and Robillard, 2013).

Female Southern Kingfish in the northcentral GOM reached sexual maturity as small as 163 mm TL, corresponding to 1 year of age. Females reached 50% maturity by 171 mm TL and 100% maturity by 211 mm TL, both at age 1. These results are consistent with reports from Smith and Wenner (1985), who estimated that females from the SAB reached TL_{50} at 192 mm TL at age 1 and TL_{100} at 230 mm TL, also at age 1. Recently, McDowell and Robillard (2013) have confirmed these estimates of TL_{50} (199 mm TL) and 50% maturity (1.1 years), indicating little change in the population of Southern Kingfish from the SAB over the past 25 years. Similarly, Haluch et al. (2011) reported female TL_{50} at 167 mm TL from the area of Santa Catarina, Brazil, with TL_{100} at 228 mm TL. In contrast, Militelli et al. (2013) found TL_{50} for females in the coastal zone of Buenos Aires, Argentina, to be 223 mm TL, although this result was based on a relatively small sample size (n=54). Harding and Chittenden (1987) noted TL_{100} at

250 mm TL (with few maturing, virgin fish past 220 mm TL) for fish in the northwestern GOM, providing further evidence that Southern Kingfish in the GOM reach sexual maturity by age 1. Many sciaenids have developed a strategy to mature in the first year of life (Waggy et al., 2006; see Appendix); 10 of the 17 species or populations analyzed in the PCA were in the low age-at-maturity quadrats of the plot (groups B, C, and D in Fig. 7).

Population-level characteristics, such as mortality rates and longevity, have been shown to correlate with individual growth parameters (Beverton and Holt, 1959; Lorenzen, 2005). Therefore, the somatic growth characteristics of Southern Kingfish discussed here provide a proxy for the determination of these characteristics that can aid in the management of the species. Our results indicate geographic differences in the maximum length and age of Southern Kingfish, as well as sex-specific differences in growth and condition.

The maximum length from our study (348 mm TL) is similar to the lengths reported by Bearden (1963) on the East Coast of the United States (338 mm TL) and by Harding and Chittenden (1987) for the northwestern GOM (345 mm TL), but this result is smaller than the maximum size of 404 mm TL (Smith and Wenner, 1985) and 419 mm TL (McDowell and Robillard, 2013) reported for fish off the Atlantic coast of the southeastern United States. In our study, males from the GOM were found to have a smaller mean size (211.2 mm TL) than that of females (238.5 mm TL). Sex-specific differences in maximum length also were reported by Harding and Chittenden (1987) and McDowell and Robillard (2013) for Southern Kingfish, and such differences are common for species in this family (Chao, 1995, 2002).

On the basis of annuli counts in sagittal otoliths, maximum age for both males and females in the northcentral GOM was 4+ years. The oldest reported Southern Kingfish was an individual that reached age 6 from the Atlantic coast of the southeastern United States (Smith and Wenner, 1985), although this age determination was made with scale annuli, which is less accurate than age determination from otoliths (VanderKooy, 2009). Recent aging of Southern Kingfish from Georgia with the use of otoliths revealed a maximum age of 5 years, with the majority of fish ≤age 3. The maximum age and sizes of Southern Kingfish estimated in this study provide additional evidence that this species is of a relatively small size and has a short life span. Many other sciaenids are typically relatively small and have a short life span (Waggy et al., 2006; see Appendix); 10 of the 17 stocks analyzed in the PCA were in the small maximum TL quadrants of the plot (groups B, C, and D in Fig. 7).

Annual ring formation in otoliths of Southern Kingfish occurred from April to May, a finding that differs from the reported marginal increments in scales by Smith and Wenner (1985), who found that the scale annulus was formed in the winter and early spring. However, analysis of otoliths from Southern Kingfish

collected in Georgia confirms that formation of annual growth rings occurs during April and May (McDowell and Robillard, 2013). The formation of the opaque annual ring has been attributed to several factors, including seasonal temperature changes, feeding patterns, wet and dry seasons, and reproductive cycles (Beckman and Wilson, 1995). On the basis of our results, formation of opaque rings in the GOM population appears to coincide with the peak of the spawning season during April–May.

Sciaenid life-history traits

Despite the fact that a number of sciaenid species are commercially and recreationally important in the continental United States, complete life-history information is available for only a small number of species. In particular, information on fecundity and spawning frequency is lacking for over half of the stocks listed in the Appendix. Such information about the reproductive traits of these stocks is one important component for understanding population dynamics (Cortés, 1998), and priority should be placed on obtaining this information for these commercially or recreationally important stocks.

All Sciaenidae exhibit some common life-history traits, such as indeterminate fecundity, batch spawning, relatively small pelagic eggs, and an estuarine-dependent juvenile phase (Chao, 2002). However, we analyzed the range for 5 reproductive and somatic traits with 2 principal component axes and explained 68.1% of the variation among species. This result is lower than the 91% total variation explained by Winemiller and Rose (1992) with analysis of 5 traits on 3 principal component axes for 147 fish species representing multiple families, but variation in life history is reduced when analyzing traits of species within a single family. Waggy et al. (2006) examined the relationships among 8 life-history variables in 11 sciaenid species occurring in the GOM and Caribbean and found that 2 principal components explained 86% of the variance, although several of the variables they included in their analysis were correlated. We have determined that the components of our analysis represent size-related aspects of life history (PC 1) and spawning season dynamics (PC 2), both of which combine somatic and reproductive traits. Winemiller and Rose (1992) and Waggy et al. (2006) identified similar components in their life-history analyses.

We identified 5 distinct sciaenid groups on the basis of the PCA analysis (see Fig. 7), indicating these groups of species are very similar to each other. The 2 largest sciaenids in the analysis, Red Drum and Black Drum from the GOM, compose group A and have similar life-history traits, but they spawn at different times of the year (Murphy and Taylor, 1990; Nieland and Wilson, 1993). In group B, Sand Seatrout and Southern Kingfish are both GOM species with similar sizes, spawning seasons, and spawning frequencies, but Sand

Seatrout is a more pelagic species that spawns in the nearshore GOM (Shlossman and Chittenden, 1981), whereas Southern Kingfish tend to be benthic and estuarine spawners, on the basis of the common occurrence of young fish in estuaries (Anderson et al., 2012). The Atlantic population of Southern Kingfish also is included in this group, indicating that geographic differences among a single species, although present, do not result in changes in basic life-history strategies. The inclusion of White Croaker of the Pacific in this same group indicates similar strategies across widely spaced regions.

Group C consists of the species with the highest RBF, Spot and Silver Perch; both species occur in the GOM but have different spawning seasons and locations (Cowan and Shaw, 1988; Grammer et al., 2009) and therefore reduce potential competition among larvae. The GOM species Atlantic Croaker and Silver Seatrout are both in group D but have different spawning seasons (White and Chittenden, 1977; DeVries and Chittenden, 1982), and the Atlantic population of Atlantic Croaker is found in this same group. Within group E, the Atlantic congeners Spotted Seatrout and Weakfish and the Pacific species Spotfin Croaker, and Yellowfin Croaker have similar spawning seasons and habitats within regions (Brown, 1981; Lowerre-Barbieri et al., 1996a; Miller et al., 2009), indicating that life-history traits among this group are very similar. Geographic differences in life-history parameters between Atlantic and GOM Spotted Seatrout (Brown, 1981; Murphy and Taylor, 1994; Brown-Peterson, 2003) appear to be once again less important than overall life-history strategies.

For all 3 of the sciaenid species that have both Atlantic and GOM populations—the Southern Kingfish, Atlantic Croaker, and Spotted Seatrout— those populations are in the same groups as their conspecifics, but those 3 species are in 3 different life-history groups within the PCA. Therefore, the similarity of overall within-species life-history strategies appears to override observed differences in reproductive seasons with latitude (Brown-Peterson and Thomas, 1988; Conover, 1992).

Overall, the PCA results indicate that groups A and E can be characterized as having a periodic or *K* life-history strategy but that group C has an opportunistic or *r* strategy (sensu Winemiller and Rose, 1992). Groups B and D (8 species) do not fit classic definitions of life-history strategies, indicating that strategies of smaller sciaenids with low fecundity may be more susceptible to environmental or physiological variation than larger sciaenids with high fecundity. Indeed, the importance of behavioral and physiological factors should be considered when evaluating life-history variation (Ricklefs and Wikelsik, 2002) because some observed variations may be a result of physiological sensitivity or behavioral control mechanisms that are related to the environment.

Conclusions

We examined the somatic and reproductive life-history characteristics of Southern Kingfish and described how the parameters in this multivariate set relate to the parameters of other species of Sciaenidae that are encountered by recreational and commercial fisheries in the continental United States. This study shows that Southern Kingfish is a generally short-lived, early maturing fish with a longer spawning season than that of other Sciaenidae and that it exhibits significant sex-specific differences in somatic characteristics. The multivariate analysis that we used in this study also indicates that relationships of demographic characteristics within this family are complex. Such complexity is mediated by both evolutionary and ecological processes. Our inventory of life-history characteristics of sciaenid species indicates a number of gaps in available data. Demographic data that are missing or that are collected and reported but that are not sex specific may, to some extent, compromise the use of among-population comparisons.

Acknowledgments

Literature cited

Anderson, E. J., B. H. Comyns, H. M. Perry, and C. F. Rakocinski.
2012. Early growth of three kingfish (*Menticirrhus*) species found in coastal waters of the northern Gulf of Mexico. Gulf Caribb. Res. 24:23–29.

Bagenal, T. B.
1966. The ecological and geographical aspects of fecundity of the plaice. J. Mar. Biol. Assoc. U.K. 46:161–168.

Bagenal, T. B., and E. Braum.
1971. Eggs and early life history. *In* Methods for assessment of fish production in fresh waters (W. E. Ricker, ed.), p. 159–181. International Biological Program Handbook No. 3, 2nd ed. Blackwell Scientific Publs., Oxford, U.K..

Barbieri, L. R., M. E. Chittenden Jr., and S. K. Lowerre-Barbieri.
1994. Maturity, spawning and ovarian cycle of Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay and adjacent coastal waters. Fish. Bull. 92:671–685.

Barger, L. E.
1985. Age and growth of Atlantic croakers in the northern Gulf of Mexico, based on otolith sections. Trans. Am. Fish. Soc. 114:847–850.

Bearden, C. W.
1963. A contribution to the biology of the king whiting, genus *Menticirrhus* of South Carolina. Contr. Bears Bluff Lab. 38:1–27.

Beckman, D. W., and C. A. Wilson.
1995. Seasonal timing of opaque zone formation in fish otoliths. *In* Recent development in fish otolith research (D. H. Secor, J. M. Dean, and S. E. Campana, eds.), p. 27–43. Belle W. Baruch Library of Marine Science 19, Univ. South Carolina Press, Columbia, SC.

Beckman, D. W., A. L Stanley, J. H. Render, and C. A. Wilson.
1990. Age and growth of black drum in Louisiana USA waters of the Gulf of Mexico. Trans. Am. Fish. Soc. 119:537–544.

Beverton, R. J. H., and S. J. Holt.
1959. A review of the lifespans and mortality rates of fish in nature and the relation to growth and other physiological characteristics. *In* Ciba Foundation Symposium—The lifespan of animals (colloquia on ageing), vol. 5 (G. E. W. Wolstenholme and M. O'Conner), p.142–177. Jon Wiley & Sons, Ltd., Chichester, U.K.

Brown, N. J.
1981. Reproductive biology and recreational fishery for spotted seatrout, *Cynoscion nebulous*, in the Chesapeake Bay area. M.A. thesis, 120 p. College of William and Mary, Gloucester Point, VA.

Brown-Peterson, N. J.
2003. The reproductive biology of the spotted seatrout. *In* The biology of spotted seatrout (S. A. Bortone, ed.), p. 99–133. Marine Biology Series. CRC Press, Boca Raton, FL.

Brown-Peterson, N., and P. Thomas.
1988. Differing reproductive life histories between temperate and subtropical groups of *Cynoscion nebulosus*. Contrib. Mar. Sci. 30(suppl.):71–78.

Brown-Peterson, N. J., and J. W. Warren.
2001. The reproductive biology of spotted seatrout, *Cynoscion nebulosus*, along the Mississippi Gulf Coast. Gulf Mex. Sci. 19:61–73.

Brown-Peterson, N. J., D. M. Wyanski, F. Saborido-Rey, B. J. Macewicz, and S. K. Lowerre-Barbieri.
2011. A standardized terminology for describing reproductive development in fishes. Mar. Coast. Fish. 3:52–70.

Chao, N. L.
1995. Sciaenidae. Corvinas, barbiches, bombaches, corvinatas, corvinetas, corvinillas, lambes, pescadillas, roncachos, verrugatos. *In* Guia FAO para identificacion de especies para los fines de la pesca. Pacifico Centro-oriental, volume III, Vertebrados—parte 2 (W. Fischer, F. Krupp, W. Schneider, C. Sommer, K. E. Carpenter, and V. Niem, eds.), p. 1427–1518. Organizacion De Las Naciones Unidas Para La Agricultura y La Alimentacion, Roma, Italia.
2002. Sciaenidae. *In* The living marine resources of the western central Atlantic, vol 3: Bony fishes part 2 (Opistognathidae to Molidae), sea turtles and marine mammals (K. E. Carpenter, ed.), p. 1583–1653. FAO, Rome.

Chavance, P., D. Flores, A. Yañez-Arancibia, and F. Amezcua.
1984. Ecología, biología y dinámica de las poblaciones *Bairdiella chrysoura* en la Laguna de Términos, sur del Golfo de México (Pisces: Sciaenidae). Anal. Inst. Cien. Mar Limnol. UNAM 11:123–162.

Comyns, B. H., J. Lyczkowski-Shultz, D. L. Nieland, and C. A. Wilson.
    1991. Reproduction of red drum, *Sciaenops ocellatus*, in the north-central Gulf of Mexico: seasonality and spawner biomass. *In* Larval fish recruitment and research in the Americas: proceedings of the thirteenth annual fish conference 21–26 May 1989, Merida, Mexico (R. H. Hoyt, ed.), p. 17–26. NOAA Tech. Rep. NMFS 95.

Conover, D.
    1992. Seasonality and the scheduling of life history at different latitudes. J. Fish Biol. 41:161–178.

Cortés, E.
    1998. Demographic analysis as an aid in shark stock assessment and management. Fish. Res. 39:199–208.

Cowan, J. H., Jr., and R. F. Shaw.
    1988. The distribution, abundance, and transport of larval sciaenids collected during winter and early spring from the continental shelf water off west Louisiana. Fish. Bull. 86:129–142.

Crowe, B. J.
    1984. Distribution, length-weight relationship, and length-frequency data of southern kingfish, *Menticirrhus americanus,* in Mississippi. Fish. Bull. 82:427–434.

DeMartini, E. E.
    1990. Annual variations in fecundity, egg size, and the gonadal and somatic conditions of queenfish *Seriphus politus* (Sciaenidae). Fish. Bull. 89:9–18.

DeMartini, E. E., and R. K. Fountain.
    1981. Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: attributes representative of serial spawning fishes. Fish. Bull. 79:547–560.

DeVries, D. A., and M. E. Chittenden Jr.,
    1982. Spawning, age determination, longevity, and mortality of the silver seatrout, *Cynoscion nothus*, in the Gulf of Mexico. Fish. Bull. 80:487–498.

Ditty, J. G.
    1986. Ichthyoplankton in neritic waters of the northern Gulf of Mexico off Louisiana: Composition, relative abundance, and seasonality. Fish. Bull. 84:935–946.

Ditty, J. G., G. G. Zieske, and R. F. Shaw.
    1988. Seasonality and depth distribution of larval fishes in the northern Gulf of Mexico above latitude 26°00′N. Fish. Bull. 86:811–823.

Ditty, J. G., M. Bourgeois, R. Kasprzak, and M. Konikoff.
    1991. Life history and ecology of sand seatrout *Cynoscion arenarius* Ginsburg, in the northern Gulf of Mexico: a review. Northeast Gulf Sci. 12:35–47.

Eschmeyer, W. N., E. S. Herald, and H. Hammann.
    1983. A field guide to Pacific coast fishes of North America, 336 p. The Peterson Field Guide Series, Houghton Mifflin Co., Boston.

Fabens, A. J.
    1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29:265–289.

Field, A.
    2005. Discovering statistics using SPSS, 2nd ed., 779 p. Sage Publications, Ltd., London.

Fitzhugh, G. R., B. A. Thompson, and T. G. Snider III.
    1993. Ovarian development, fecundity, and spawning frequency of black drum *Pogonias cromis* in Louisiana. Fish. Bull. 91:244–253.

Fulford, R. S., and J. R. Hendon.
    2010. Evaluating management actions for spotted seatrout, *Cynoscion nebulosus,* in Mississippi with an age-structured projection model. Gulf Carib. Res. 22:51–61.

Goldberg, S. R.
    1976. Seasonal spawning cycles of the sciaenid fishes *Genyonemus lineatus* and *Seriphus politus*. Fish. Bull. 74:983–985.
    1981. Seasonal spawning cycle of the black croaker, *Cheilotrema saturnum* (Sciaenidae). Fish. Bull. 79:561–562.

Grammer, G. L., N. J. Brown-Peterson, M. S. Peterson, and B. H. Comyns.
    2009. Life history of silver perch *Bairdiella chrysoura* (Lacepede 1803) in north-central Gulf of Mexico estuaries. Gulf Mex. Sci. 27:62–73.

Greeley, M. S., Jr., K. R. Marion, and R. MacGregor.
    1986. Semilunar spawning cycles of *Fundulus similis* (Cyprinodontidae). Environ. Biol. Fishes 17:125–131.

Hair, J. F., Jr., R. E. Anderson, R. L. Tatham, and E. J. Grablowsky.
    1984. Multivariate data analysis, with readings, 360 p. Macmillan Publ., Inc., New York.

Haluch, C. F., V. Abilhoa, M. O. Freitas, M. F. M. Correa, and M. Hostim-Silva.
    2011. Estrutura populacional e biologia reproductive de *Menticirrhus americanus* (Linnaeus, 1758) (Teleostei, Sciaenidae) no baia de Ubatuba-Enseada, Santa Catarina, Brasil. Biotemas 24:47–59.

Harding, S. M., and M. E. Chittenden Jr.
    1987. Reproduction, movements, and population dynamics of the Southern Kingfish, *Menticirrhus americanus*, in the northwest Gulf of Mexico. NOAA Tech. Rep. NMFS 49, 21 p.

Hart, J. L.
    1973. Pacific fishes of Canada. Fish. Res. Board Can. Bull. 180, 740 p.

Hildebrand, S. F., and L. E. Cable.
    1934. Reproduction and development of whitings or king fishes, drums, spot, croaker, and weakfishes or sea trouts, family Sciaenidae of the Atlantic coast of the United States. Bull. U.S. Bur. Fish. 48:41–117.

Hunter, J. R., and B. J. Macewicz.
    1985. Measurement of spawning frequency in multiple spawning fishes. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax* (R. Lasker, ed.), p. 79–94. NOAA Tech. Rep. NMFS 36.

Irwin, R. J.
    1970. Geographical variation, systematics, and general biology of shore fishes of the genus *Menticirrhus*, family Sciaenidae. Ph.D. diss., 292 p. Tulane Univ., New Orleans, LA.

Joseph, D. C.
    1962. Growth charateristics of two southern California surffishes, the California corbina and spotfin croaker, family Sciaenidae. Fish Bull. Calif. Dep. Fish Game 119:1–54.

Kobylanski, G. J., and P. F. Sheridan.
    1979. Distribution, abundance, feeding and long-term fluctuations of spot, *Leiostomus xanthurus*, and croaker, *Micropogonias undulatus*, in Apalachicola Bay, Florida, 1972–1977. Contrib. Mar. Sci. 22:149–162.

Lorenzen, K.
    2005. Population dynamics and potential of fisheries stock enhancement: practical theory for assessment and policy analysis. Philos. Trans. R. Soc. Lond., Ser. B: Biol. Sci. 360:171–189.

Love, M. S., G. E. McGowen, W. Westphal, R. J. Lavenberg, and L. Martin.
  1984. Aspects of the life history and fishery of the white croaker, *Genyonemus lineatus* (Sciaenidae), off California. Fish. Bull. 82:179–198.
Lowerre-Barbieri, S. K., M. E. Chittenden Jr., and L. R. Barbieri.
  1996a. Variable spawning activity and annual fecundity of weakfish in Chesapeake Bay. Trans. Am. Fish. Soc. 125:532–545.
  1996b. The multiple spawning pattern of weakfish in the Chesapeake Bay and Middle Atlantic Bight. J. Fish Biol. 48:1139–1163.
Lowerre-Barbieri, S. L., N. Henderson, J. Llopiz, S. Walters, J. Bickford, and R. Muller.
  2009. Defining a spawning population (*Cynoscion nebulosus*) over temporal, spatial, and demographic scales. Mar. Ecol. Prog. Ser. 394:231–245.
McDowell, D. E., and E. Robillard.
  2013. Life history characteristics and age validation of southern kingfish (*Menticirrhus americanus* (Linnaeus, 1758)) in the middle South Atlantic Bight. J. Appl. Ichthyol. 29:839–846.
Militelli, M. I., J. G. Macchi, and K. A. Rodriguez.
  2013. Comparative reproductive biology of Sciaenidae family species in the Río de la Plata and Buenos Aires Coastal Zone, Argentina. J. Mar. Biol. Assoc. U.K. 93:413–423.
Miller, E. F., L. G. Allen, D. J. Pondella II, and K. T. Herbinson.
  2008. The life history and ecology of black croaker, *Cheilotrema saturnum*. CalCOFI Rep. 49:191–201.
Miller, E. F., S. Goldberg, J. Nunez, N. Burkes, and J. Kuratomi.
  2009. The reproductive biology of two common surf-zone associated sciaenids, yellowfin croaker (*Umbrina roncador*) and spotfin croaker (*Roncador stearnsii*), from southern California. Bull. South. Calif. Acad. Sci. 108(3):152–159.
Morse, W. W.
  1980. Maturity, spawning, and fecundity of Atlantic croaker, *Micropogonias undulatus*, occurring north of Cape Hatteras, North Carolina. Fish. Bull. 78:190–195.
Murphy M. D., and R. G. Taylor.
  1990. Reproduction, growth, and mortality of red drum *Sciaenops ocellatus* in Florida waters. Fish. Bull. 88:531–542.
  1994. Age, growth, and mortality of spotted seatrout in Florida waters. Trans. Am. Fish. Soc. 123:482–497.
Nieland, D. L., and C. A. Wilson.
  1993. Reproductive biology and annual variation of reproductive variables of black drum in the northern Gulf of Mexico. Trans. Am. Fish. Soc. 122:318–327.
Nieland, D. L., R. G. Thomas, and C. A. Wilson.
  2002. Age, growth, and reproduction of spotted seatrout in Barataria Bay, Louisiana. Trans. Am. Fish. Soc. 131:245–259.
Nielsen, L. A., and D. L. Johnson.
  1983. Fisheries techniques, 301 p. Am. Fish. Soc., Bethesda, MD.
Nye, J. A., and T. E. Targett.
  2008. Reproductive characteristics of weakfish in Delaware Bay: implications for management. N. Am. J. Fish. Manage. 27:1–11.

Page, L. M., H. Espinosa-Perez, L. T. Findley, C. R. Gilbert, R. N. Lea, N. E. Mandrak, R. L. Mayden, and J. S. Nelson.
  2013. Common and scientific names of fishes from the United States, Canada and Mexico, Special Publication 34, 384 p. Am. Fish. Soc., Bethesda, MD.
Pattillo, M. E., T. E. Czapla, D. M. Nelson, and M. E Monaco.
  1997. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, volume II: species life history summaries, 377 p. ELMR Rep. No. 11. NOAA/NOS Strategic Environmental Assessment Division, Silver Spring, MD.
Pondella, D. J., II, J. T. Froeschke, L. S. Wetmore, E. Miller, C. F. Valle, and L. Medeiros.
  2008. Demographic parameters of yellowfin croaker, *Umbrina roncador* (Perciformes: Sciaenidae), from the southern California Bight. Pac. Sci. 62:555–568.
R Core Team.
  2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available from http://www.R-project.org, accessed June, 2012.]
Reid, G. K, Jr.
  1954. An ecological study of the Gulf of Mexico fishes, in the vicinity of Cedar Key, Florida. Bull. Mar. Sci. Gulf Caribb. 4:1–12.
Ricker, W. E.
  1979. Growth rates and models. *In* Fish physiology, volume VIII: bioenergetics and growth (W. S. Hoar, D. J. Randall, and J. R. Brett, eds.), p. 677–743. Academic Press, New York.
Ricklefs, R. E., and M. Wikelsik.
  2002. The physiology/life-history nexus. Trends Ecol. Evol. 17:462–468.
Ross, S. W.
  1988. Age, growth, and mortality of Atlantic croaker in North Carolina, with comments on population dynamics. Trans. Am. Fish. Soc. 117:461–473.
Shanks, A. L., and G. L. Eckert.
  2005. Population persistence of California Current fishes and benthic crustaceans: a marine drift paradox. Ecol. Monogr. 75:505–524.
Sheridan, P. F., D. L. Trimm, and B. M. Baker.
  1984. Reproduction and food habits of seven species of northern Gulf of Mexico fishes. Contrib. Mar. Sci. 27:175–204.
Shlossman, P. A., and M. E. Chittenden Jr.
  1981. Reproduction, movements, and population dynamics of the sand seatrout, *Cynoscion arenarius*. Fish. Bull. 79:649–669.
Smith, J. W., and C. A. Wenner.
  1985. Biology of the southern kingfish in the South Atlantic Bight. Trans. Am. Fish. Soc. 114:356–366.
Thomas, J.
  1968. Management of the white seabass (*Cynoscion nobilis*) in California waters. Fish Bull. Calif. Dep. Fish Game 142:1–34
VanderKooy, S. J. (ed.).
  2009. A practical handbook for determining the age of Gulf of Mexico fishes, 2nd ed. Gulf States Mar. Fish. Comm. Publ. No. 167, 157 p.
Waggy, G. L., N. J. Brown-Peterson, and M. S. Peterson.
  2006. Evaluation of the reproductive life history of the Sciaenidae in the Gulf of Mexico and Caribbean Sea: "greater" versus "lesser" strategies? Proc. Gulf Caribb. Fish. Inst. 57:263–281.

White, M. L., and M. E. Chittenden.
    1977. Age determination, reproduction, and population dynamics of the Atlantic croaker, *Micropogonias undulatus*. Fish. Bull. 75:109–123.
Williams, J. P., J. T. Claisse, and D. J. Pondella II.
    2012. Patterns of life history and habitat use of an important recreational fishery species, spotfin croaker, and their potential fishery implications. Mar. Coast. Fish. 4:71–84.
Wilson, C. A., and D. L. Nieland.
    1994. Reproductive biology of red drum, *Sciaenops ocel-*

latus, from the neritic waters of the northern Gulf of Mexico. Fish. Bull. 92:841–850.
Winemiller, K. O.
    2005. Life history strategies, population regulation, and implications for fisheries management. Can. J. Fish. Aquat. Sci. 62:872–885.
Winemiller, K. O., and K. A. Rose.
    1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Can. J. Fish. Aquat. Sci. 49:2196–2218.

Appendix

Table of sciaenid species in the U.S. Exclusive Economic Zone and life history metrics used in this study. An asterisk (*) indicates that values are reported for Gulf of Mexico (GOM) and Atlantic stocks combined. TL=total length, FL=fork length, SL=standard length, F=female, p=pooled, mo=months, y=years. Morphology Index (*b*) is defined as the exponent of weight at length from the power function. A dash alone indicates that no data were available. The species include White Seabass (*Atractoscion nobilis*), Silver Perch (*Bairdiella chrysoura*), Black Croaker (*Cheilotrema saturnum*), Sand Seatrout (*Cynoscion arenarius*), Spotted Seatrout (*Cynoscion nebulosus*), Silver Seatrout (*Cynoscion nothus*), Shortfin Corvina (*Cynoscion parvipinnis*), Weakfish (*Cynoscion regalis*), White Croaker (*Genyonemus lineatus*), Spot (*Leiostomus xanthurus*), Southern Kingfish (*Menticirrhus americanus*), Gulf Kingfish (*Menticirrhus littoralis*), Northern Kingfish (*Menticirrhus saxatilis*), California Corbina (*Menticirrhus undulatus*), Atlantic Croaker (*Micropogonias undulatus*), Black Drum (*Pogonias cromis*), Spotfin Croaker (*Roncador stearnsi*), Red Drum (*Sciaenops ocellatus*), Queenfish (*Seriphus politus*), and Yellowfin Croaker (*Umbrina roncador*). *x*=mean value.

Species	Region	Max age (y)	Max length (TL$_\infty$) (mm TL)	Spawning-season duration (mo)	Spawning frequency (d)	Relative fecundity (eggs g^{-1} ovary-free body weight)	Age at maturity (y)	Size at maturity (mm)	Morphology index (*b*)	References
White Seabass	Pacific	20	1660	6–8	–	–	4	610 TL	2.94	7,22,41,44
Silver Perch	GOM	4–5	250	3	1.3–1.6	863	0+	110–120 TL	2.93 (F)	8,21
Black Croaker	Pacific	21	394	5	–	–	1+	182 TL	2.92	20,30
Sand Seatrout [a]	GOM	3	(574)	7	2.8	348	0+ to 1	147 SL	3.08 to 3.24 (F)	16,42,43
Spotted Seatrout	Atlantic	15	796 (854)	3–5	3.2–6.5	319	1–2	280–350 TL	2.99 (F)	5,6,34
	GOM	9	712 (817)	6–6.5	2.6–5	250–650	1	245–285 TL	2.86 (F)	6,34,36
Silver Seatrout	GOM	1.5	380	5.5	–	878	0+	123–164 TL	3.01(p)	13,42
Shortfin Corvina	Pacific	–	690	–	–	–	–	–	3.00	23
Weakfish	Atlantic	8	950	3.5	2.6–12.6	375–880	1	170 TL	2.86 to 2.98	27, 28, 37
White Croaker	Pacific	13–15	410–432	7–10	5	19–180	1	130–150 TL	2.94	19,22,26,41
Spot	GOM	2–3, 5	250	5	–	267–2948 (*x*=1607)	1+	127 TL	2.95 (p)	10,38,42
Southern Kingfish	Atlantic	5	418.9 (F) 290.7 (M)	6	2.0–4.2	309	1.1	199 TL	3.13 [b,c]	29
	GOM	4+	348 (303)	6	6.9	231	1	171 TL	3.17 (F)	This study
Gulf Kingfish	*	2	483	4	–	–	–	210 TL	2.87(p)	1, 23
Northern Kingfish	*	4	450–500	–	–	–	1	186–230 TL	3.08(p)	1
California Corbina	Pacific	8	710	5	–	–	3 (F)	325 TL	3.07 (p)	17,24,41
Atlantic Croaker	Atlantic	7	521	6	–	1240–1818 (*x*=1529)	1+	173 TL	3.23 (p)	2,32,40
	GOM	3–5, 8	369	4–8	–	519–1581 (*x*=1050)	1+	140–170 TL	3.14 (p) or 2.87(p)	3,10,14,15,25, 38,42,45
Black Drum	GOM	43	1500	2, 4	3–4	67–793	5	600–649 FL	3.05 (p)	4,18,33, 35
Spotfin Croaker [d]	Pacific	24	675–700	4	–	545	3 (F)	312 TL	2.94 (p)	7,24,31,46
Red Drum	Atlantic	33	1119	3	–	–	6	900 TL	3.03 (F)	33
	GOM	24	992	3	2–4	42–447	4	700 TL	3.10 (F)	9,33,47

Appendix continued

Queenfish [d]	Pacific	12	(198)	6	7.4	264–366	2	106–110 SL	2.85 to 3.15	11,12,19
Yellowfin Croaker [d]	Pacific	15	560 (313)-F	3	–	489	1.5 (F)	140 SL	3.02	31,39

Key to references: 1=Armstrong and Muller, 1996; 2=Barbieri et al., 1994; 3=Barger, 1985; 4=Beckman et al., 1990; 5=Brown, 1981; 6=Brown-Peterson, 2003; 7=Chao, 1995; 8=Chavance et al., 1984; 9=Comyns et al., 1991; 10=Cowan and Shaw, 1988; 11=DeMartini, 1990; 12=DeMartini and Fountain, 1981; 13=DeVries and Chittenden, 1982; 14=Ditty, 1986; 15=Ditty et al., 1988; 16=Ditty et al., 1991; 17=Eschmeyer et al., 1983; 18=Fitzhugh et al., 1993; 19=Goldberg, 1976; 20=Goldberg, 1981; 21=Grammer et al., 2009; 22=Hart, 1973; 23=Joseph, 1962; 24=Kobylanski and Sheridan, 1979; 25=Love et al., 1984; 26=Lowerre-Barbieri et al., 1996a; 27=Lowerre-Barbieri et al., 1996b; 28=McDowell and Robillard, 2013; 29=Miller et al., 2008; 30=Miller et al., 2009; 31=Morse, 1980; 32=Murphy and Taylor, 1990; 33=Murphy and Taylor, 1994; 34=Nieland and Wilson, 1993; 35=Nieland et al., 2002; 36=Nye and Targett, 2008; 37=Pattillo et al., 1997; 38=Pondella et al., 2008; 39=Ross 1988; 40=Shanks and Eckert, 2005; 41=Sheridan et al., 1984; 42=Shlossman and Chittenden, 1981; 43=Thomas, 1968; 44=White and Chittenden, 1977; 45=Williams et al., 2012; 46=Wilson and Nieland, 1994.

[a] Warren, J. R., and N. J. Brown-Peterson.
   2003. Sport fish studies in Mississippi coastal waters, job 1. Final Rep. Project F-131, 30 p. [Available from Mississippi Department of Marine Resources, 1141 Bayview Ave., Biloxi, MS 39532.]
[b] McDowell, D. E.
   2013. Unpubl. data. Coastal Resources Division, Georgia Department of Natural Resources, One Conservation Way, Brunswick, GA 31520.
[c] Robillard, E.
   2013. Unpubl. data. Northeast Fisheries Science Center, National Marine Fisheries Service, Woods Hole, MA 02543-1026.
[d] Miller, E. F., C. T. Mitchell, D. J. Pondella II, and S. Goldberg.
   2011. Life history parameters of common southern California marine fish subject to entrainment. Final Rep. CEC-500-2011-008, 42 p. [Available from Energy-Related Environmental Research Program, Public Interest Energy Research (PIER), California Energy Commission, 1516 Ninth St., MS-29, Sacramento, CA 95814-5512.]
[e] IGFA (International Game Fish Association). 2001. Database of IGFA angling records until 2001. IGFA, 300 Gulf Stream Way, Dania Beach, FL 33004.