



## Life history characteristics and age validation of southern kingfish (*Menticirrhus americanus* (Linnaeus, 1758)) in the middle South Atlantic Bight

By D. E. McDowell and E. Robillard<sup>1</sup>

Georgia Department of Natural Resources, Coastal Resources Division, One Conservation Way, Brunswick, GA, USA

### Summary

The purpose of this study was to determine critical components of the life history including otolith age validation, growth estimation, and reproductive characteristics for southern kingfish *Menticirrhus americanus*. A total of 2233 southern kingfish were collected from March 2009 to December 2010. Ages were estimated and validated using thin-sectioned otoliths. Marginal increment analysis showed a single annulus was deposited once a year between April and May. Growth was significantly different ( $P < 0.0001$ ) between sexes  $L_{inf} = 418.97 \pm 16.58$  mm,  $k = 0.29 \pm 0.03$ ,  $t_0 = -1.30 \pm 0.10$  for females and  $L_{inf} = 290.74 \pm 6.93$  mm,  $k = 0.52 \pm 0.05$ ,  $t_0 = -1.08 \pm 0.11$  for males. Southern kingfish spawn from March to August with a peak spawn in April. Based on evidence of multiple oocyte maturation stages and post-ovulatory follicles (POFs) southern kingfish are multiple spawners exhibiting indeterminate fecundity. Spawning frequency for females ranging from 222 to 351 mm TL (age 1–5) was estimated as one spawning event every 2.0–4.2 days with up to 6 million total ova produced per spawning season per female.

### Introduction

The southern kingfish, *Menticirrhus americanus*, is a ubiquitous, demersal, euryhaline teleost (Bearden, 1963; Dahlberg, 1972) found throughout nearshore waters from New York to Texas (Hildebrand and Cable, 1934; Sikora and Sikora, 1982; Smith and Wenner, 1985). Southern kingfish are considered a game fish as well as a popular food source wherever they are captured (Bearden, 1963). Of the three kingfish species caught commercially along the southeastern coast of the United States, the southern kingfish is the most landed with an average of 600 tonnes per year over the past 20 years (National Marine Fisheries Service, pers. comm.). They are also commonly caught by sport fishermen along beaches (Schaefer, 1965; Smith and Wenner, 1985) and total landings of southern kingfish have more than tripled since the 1980s; fisheries managers are concerned this increased fishing pressure may lead to a decline in the population.

The most recent ageing methodology for this species is based on scales (Smith and Wenner, 1985). In most species, scales tend to be less precise than otoliths (Campana and Nielson, 1985) and can lead to inaccuracies in assigning ages (Wilson, 2000). Other studies of southern kingfishes estimated ages from length-frequencies (Hildebrand and Cable,

1934; Bearden, 1963; Dahlberg, 1972; Harding and Chittenden, 1987). Because of the protracted spawning season and subsequent overlap in age classes, there is no confirmation that length frequency modes coincide with assigned age classes (Campana, 2001). Sagittal otoliths have not been used to age southern kingfish in the South Atlantic Bight (SAB). However, there is no evidence or *a priori* reason that otoliths would not be suitable or useful for growth studies for this species. If any comprehensive stock assessment and population modeling is to be conducted on southern kingfish, age determinations need to be accurate and precise over the fully exploited age classes (Beamish and McFarlane, 1983; Campana, 2001).

Another management issue for this species is the uncertainty of the reproductive area, seasonality and periodicity. Hildebrand and Cable (1934) suggest spawning occurs in nearshore ocean waters based on the high abundance of young-of-year (YOY) being captured along the shores of Beaufort, North Carolina. However, Bearden (1963) suspects that spawning occurs mostly or entirely offshore based on: 1) the lack of females with ripe ovaries found in inshore waters; and 2) anecdotal reports from shrimp fishermen that southern kingfish caught offshore during spring and summer appeared to be spawning. Early studies based on recruitment of southern kingfish indicate a protracted spawning season (Hildebrand and Cable, 1934; Bearden, 1963). Miller and Jorgensen (1969) found that the spawning season ranged from April through October; however, Dahlberg (1972) and Smith and Wenner (1985) found the season might actually be shorter, ranging from April through August. Frequency of young southern kingfish captured in trawls implies that the height of spawning occurs during June and July (Bearden, 1963) and into August (Hildebrand and Cable, 1934). It is also suggested southern kingfish may have two spawning seasons (Welsh and Breder, 1923). Direct observations of adult southern kingfish ovaries are limited for the Atlantic Coast, but seem to support the theory that this species is a batch spawner. In nearshore waters from Cape Fear to Cape Canaveral, Smith and Wenner (1985) collected females with all four ovarian stages (ripening, ripe, spent, and resting) from May to August, the only study in the SAB to collect a ripe female. While the occurrence and abundance of YOY can provide some insight into the spawning area and timing, direct observations of ovaries using histology would provide a more accurate basis for determining reproductive patterns for this species.

To date, only one paper has examined the fecundity of southern kingfish; however, it was conducted in the Gulf of Mexico (Fritzsche and Crowe, 1981). Females with the highest gonadosomatic indices (GSI) were used to determine fecundity, and all oocytes 0.30 mm or larger were counted

<sup>1</sup>Present address: National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, MA, USA.

and included in the estimates (Fritzsche and Crowe, 1981). Inadvertently, this could have included oocytes that were not fully developed. Even though these females were the ripest and were collected from March to September, it is possible that some of these females had spent ovaries. Basic information on the reproductive capacity of southern kingfish in Georgia can now be determined by coupling the techniques for fecundity estimation (Luna, 1968; Hunter and Macewicz, 1985; Hunter et al., 1985; West, 1990) with appropriate age information. Fecundity estimates are critical to management and are entirely lacking for southern kingfish in the SAB.

In view of its growing importance as a harvested species, and in order to manage the fishery wisely in the future, a better understanding of the life history of southern kingfish is warranted. The purpose of this study was to determine critical components of the life history including otolith age validation, growth estimation, and determination of size- and age-at-maturity. Other objectives were to determine the spawning season as well as pattern of oocyte development, and provide estimates of batch fecundity and spawning frequency.

### Materials and methods

A total of 2233 southern kingfish (1200 females, 596 males, 437 immature) were collected on a monthly basis in all six sound systems of coastal Georgia (Wassaw, Ossabaw, Sapelo, St. Simons, St. Andrew and Cumberland) between March 2009 and December 2010 using a variety of gear which included otter trawl, longline, and hook and line. The otter trawl consisted of a 12.2 m flat otter trawl with 4.8 cm stretch-mesh webbing for the body and bag, with attached tickler chain and 24 × 11 cm trawl doors. The bottom longline consisted of a 926 m mainline of 2.5 mm diameter monofilament nylon line with 60 gangions consisting of 0.7 m of 1.6 mm diameter monofilament nylon line terminated with 12/0 circle hooks.

All specimens were measured for total length (mm TL), standard length (mm SL), and total weight (TW) to the nearest 0.1 g using an Ohaus Valour 3000 scale. For each female, gonad weight (GW) to the nearest 0.1 g was recorded and gross maturity stage based on macroscopic appearance was classified according to the criteria of Robillard et al. (2008). Gonads were preserved in 10% buffered formalin for microscopic analysis within 24 h of being collected to avoid autolysis.

**Sagittal otoliths** were excised and stored dry for age determination. The left otolith of each specimen was **embedded in a mold of epoxy resin and cured overnight. The otolith was sectioned transversely through the core then mounted** on microscope slides with cytoseal-60 mounting medium. Sections were examined using a Leica MZ-9 dissecting microscope with transmitted light and dark-field polarization at 2.5 times magnification. **Two readers independently determined the age of the sectioned otoliths.** All statistical analyses were performed using S-PLUS® (version 6.1).

Periodicity of annulus formation on sectioned otoliths was determined by marginal increment analysis (Bagenal and Tesch, 1978). Otolith measurements were made with a digital image processing system attached to a CoolSNAP™ on a Leica MZ-9 microscope using Optimas® software (Media-Cybernetics, Inc., Bethesda, MD). To prevent bias in measurements associated with the marginal increment technique, the following procedures were applied: 1) all samples were

randomized before examination; 2) two consecutive years were examined; and 3) validation of every possible age group, as suggested by Campana (2001). The translucent margin beyond the last opaque annulus was measured along the ventral side of the sulcal groove.

**A test for symmetry was used to detect systematic differences between the two readers (Hoenig et al., 1995). To measure reader otolith self-precision and age reproducibility, each reader re-aged a randomly selected subset of 110 fish from 2010. Between and within reader precision was measured using Chang's (1982) average coefficient of variation (CV) following Campana and Jones (1992).**

To evaluate variability in growth, observed length-at-age data based on otoliths were fitted with a von Bertalanffy growth function (Ricker, 1975), by non-linear least squares regression. Likelihood ratio tests (Kimura, 1980) were used to determine if differences existed between von Bertalanffy parameter estimates between sexes for mean total length-at-age data.

Gonadosomatic indices were calculated for all mature females. Of the 1200 female southern kingfish sampled, 279 female ovaries were processed for histological analysis by excising the central portion of one lobe of each gonad. Samples were embedded in paraffin, sectioned to 5–6 µm thickness and stained with Harris' hematoxylin and eosin Y. Microscopic stages of maturity and atresia were distinguished based on the histological criteria of Hunter and Macewicz (1985) and Robillard et al. (2008). The key factor in determining if a fish with only primary growth oocytes had recently spawned was the presence of atresia, thus classified as recovering and not immature.

To evaluate the most appropriate site in the ovary to subsample for batch fecundity estimates, the number of hydrated oocytes per gram was determined (Hunter et al., 1985) for each of three regions (anterior, middle, posterior) of the ovaries from 11 fish. There were no significant differences in the number of hydrated oocytes between regions (ANOVA,  $F = 0.046$ , d.f. = 2,  $P = 0.955$ ). Therefore, batch fecundity was estimated using the central region of the ovary of 36 fish that contained hydrated oocytes and was calculated as the product of the hydrated oocyte density (hydrated count/sub-sample weight) times the weight of the gonads for both lobes.

Size and age at maturity were estimated from 637 females ranging in size from 128–377 mm TL and age from 0 to 5 years. Females were considered mature when yolked oocytes were present. To prevent fish in the recovering stage from being classified as immature, only fish collected during the presumed spawning period between March and August were used in the analysis. To predict the probability that a female southern kingfish was mature based on its total length and age, maturity-at-length and -at-age was modeled using logistic regression. Binary maturity observations (0 = immature, 1 = mature) and total length and age were fitted to logistic models using the function GLM (family = binomial).

### Results

Transverse sections of southern kingfish otoliths showed annuli were clear, well defined, and easy to read. Sections had easily identifiable narrow, opaque bands that alternate with wider translucent bands beyond the opaque core to the growing edge (Fig. 1). Ages estimated from annulus counts of the 2233 southern kingfish examined ranged from 0 to

5 years of age. Of the total specimens collected, 99% were 3 years of age or less.

Marginal increment analysis revealed one annulus being formed per year (Fig. 2). Annulus formation is most evident between April and May, with the lowest marginal increment values occurring in May. Marginal increment values gradually increased from June to September. Marginal width was at a maximum between December and January. It was concluded that only one annulus was formed per year during May for southern kingfish ages 0–3. Marginal increment analysis was not possible for ages 4 and 5 due to the limited samples throughout the year.

Ages were assigned to all southern kingfish collected. There were good within-reader agreements for sectioned otolith ages (reader 1 = 100% and reader 2 = 99%) and 100% accounting for disagreements of  $\pm 1$  year (Fig. 3). The measure of reader self-precision was also high for both readers: reader 1 had a CV of 0% and reader 2 had a CV of 1.2%. Between-reader agreements for sectioned otolith ages were 99.5% overall, and 100% within a year of each other (Fig. 3). The average between-reader coefficient of variation was 0.4%. There was no evidence of systematic disagreement between reader 1 and reader 2 at the  $\alpha = 0.05$  level (test of symmetry,  $\chi^2 = 8$ , d.f. = 4,  $P = 0.09$ ).

Southern kingfish grew relatively fast from hatching to age 2, after which growth slowed, approaching an asymptote by approximately age 4 (Fig. 4). Length-at-age data were fit to von Bertalanffy growth models for each sex individually and comparisons were made between sexes. Results of likelihood-ratio tests indicated a significant difference in the overall von Bertalanffy growth models for females and males ( $\chi^2 = 38.06$ , d.f. = 3,  $P < 0.0001$ ). Growth parameters demonstrated that females grew at a faster rate and reached a greater theoretical asymptotic length than males.

Oocyte development of 279 ovaries from females ranging from 128 mm to 377 mm TL (mean  $270 \pm 2.4$  mm TL) was consistent with batch spawning. All oocyte stages were present in mature ovaries, indicating that southern kingfish exhibit asynchronous oocyte development. Additionally, the presence of hydrated oocytes along with primary and advanced oocytes in individual ovaries indicated fish were capable of spawning multiple times in a season. Similarly, ovaries with post-ovulatory follicles (POFs) also contained

advanced yolked oocytes, an indication of multiple batch spawning. Different patterns of atresia were found in ovaries, depending on when they were collected in the spawning sea-

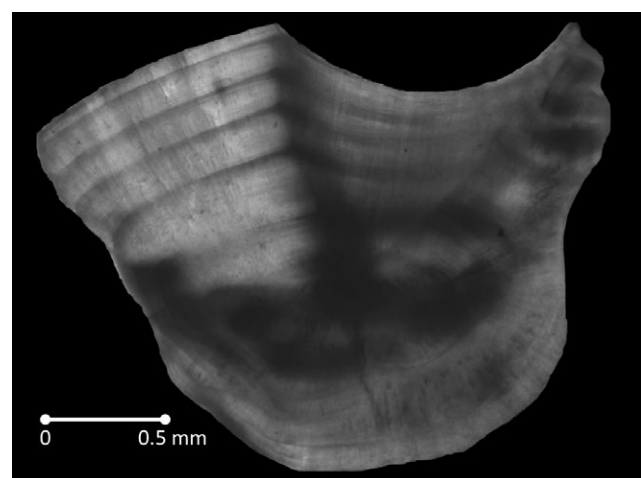


Fig. 1. Sectioned sagittal otolith from a 357 mm TL, 5-year-old female southern kingfish *Menticirrhus americanus*

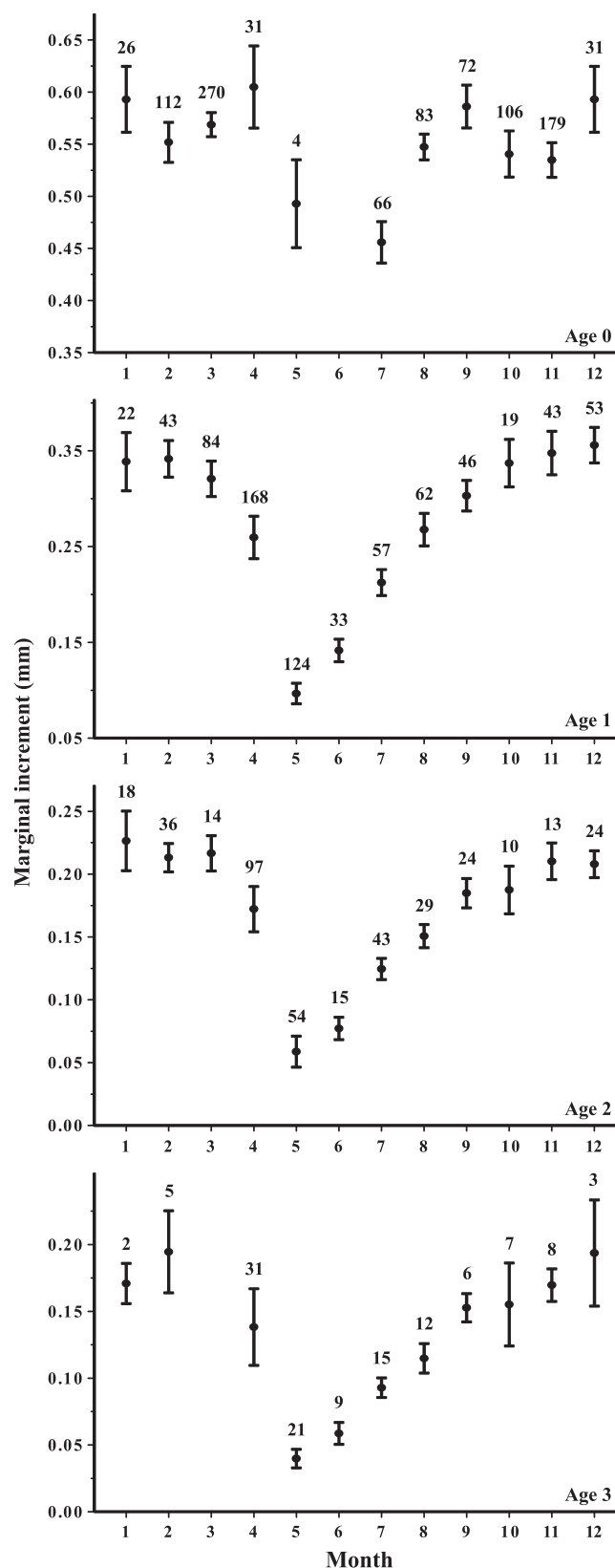


Fig. 2. Mean monthly marginal increments for southern kingfish ages 0–3 collected in 2009–2010. Vertical bars are  $\pm 1$  SE. Note changes in scales in the Y-axes.

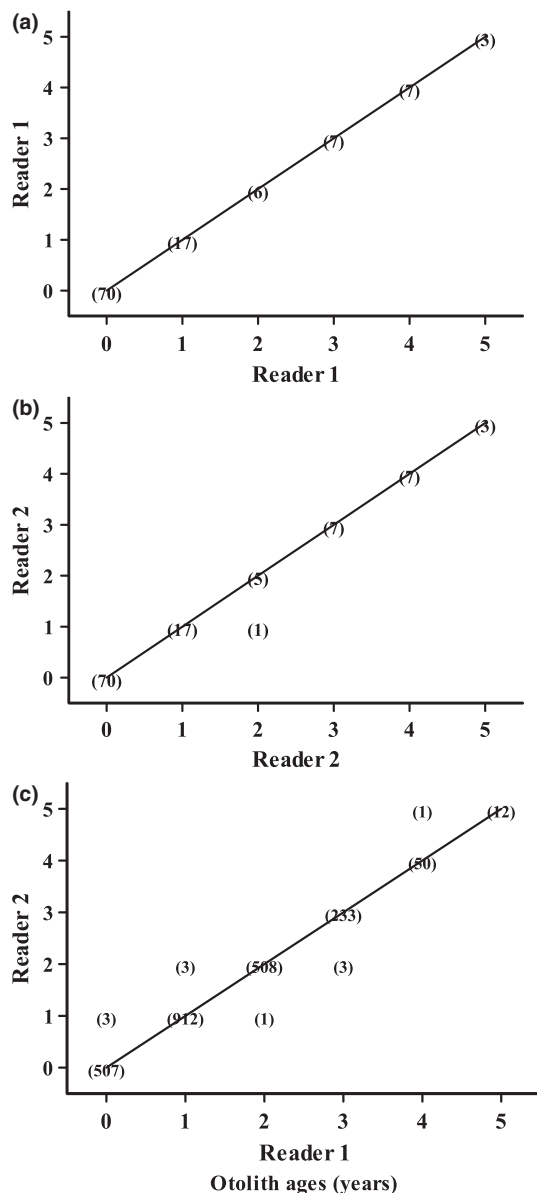


Fig. 3. Agreement plots for pair-wise comparisons between replicate annulus counts for sectioned otoliths of southern kingfish for (a) within Reader 1, (b) within Reader 2, (c) between Reader 1 and Reader 2. The 45° line represents 100% agreement. Number of observations in parentheses

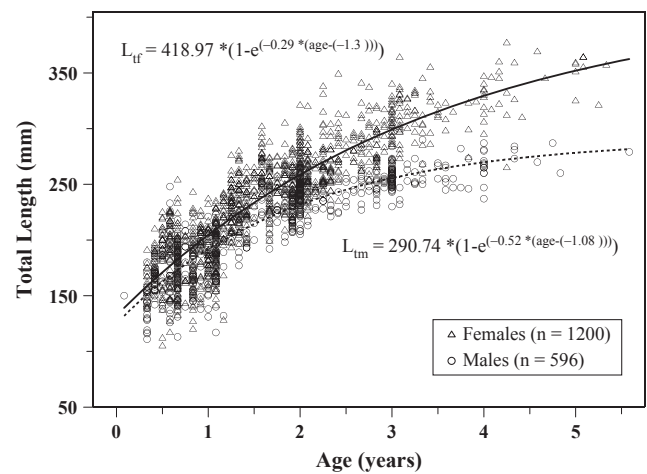


Fig. 4. Observed age-length relationship based on von Bertalanffy model for southern kingfish collected in 2009–2010 by sex (female —, male —)

son as well as between years. In 2009, ovaries indicated some early stages of atresia starting in August with surrounding healthy yolked oocytes. In 2010, atresia was evident in ovaries as early as May. For August 2009 and July 2010, cessation of spawning was indicated by gonads containing healthy primary growth oocytes, with all other oocytes being resorbed through the process of atresia. The smallest female with POFs measured 208 mm TL and 78 g TW.

Gonad development and commencement of spawning was asynchronous for southern kingfish, while cessation of spawning was synchronous. Histological analysis of mature females collected during March 2009 revealed the presence of females exhibiting either hydrated stages or early stages of vitellogenesis. By the end of the spawning season (i.e. August to early September) all mature females collected were fully spent or recovering with atretic, partially, and advanced yolked oocytes (Table 1).

Southern kingfish spawn over a broad period. Although there was some variability in GSI between years, the general seasonal pattern was repeated (Fig. 5). In 2010, mean monthly GSI was low from January to February (GSI = 0.1–1.6), but for both years increased through March (GSI = 1.0–5.9), and peaked in April (GSI = 0.5–14.6), before declining to pre-spawning levels by the end of August

Table 1

Percent maturity by year and month of the number of mature female *M. americanus* processed histologically (n). Reproductive phases, Immature: few oocytes with primary growth; developing: early vitellogenic oocytes; mature: vitellogenic oocytes; spawning: final maturation and hydrated oocytes; spent: primary to cortical alveoli with atretic yolked oocytes; recovering: primary oocytes with gamma or/and delta atretic oocytes

Stages	2009								2010								
	Mar	Apr	May	June	July	Aug	Sept	Dec	Feb	Apr	May	June	July	Aug	Sept	Oct	Nov
n	12	91	30	6	10	10	10	5	1	16	7	10	27	20	10	6	8
Immature		2%									14%	10%					
Developing	42%				10%												
Mature	16%	25%	57%	83%	90%	80%	10%			25%	43%		22%				
Gravid		2%								13%							
Spawning	42%	70%	43%	17%						56%	14%		4%				
Spent						20%	50%			29%	90%	63%	80%	100%	33%		
Recovering							40%	100%	100%	6%		11%	20%		67%	100%	



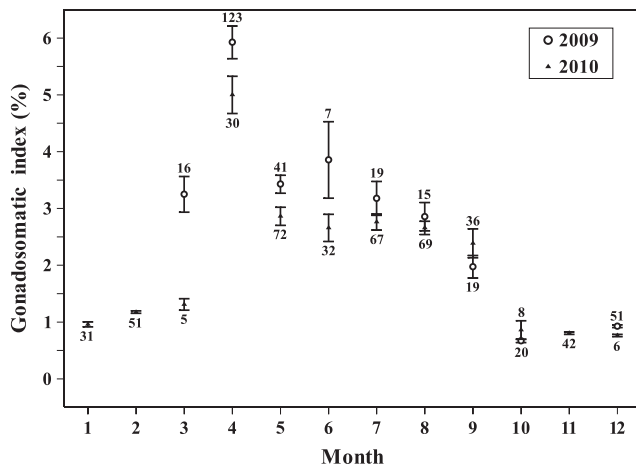


Fig. 5. Mean gonadosomatic index (GSI) by month,  $\pm 1$  SE and range of values for mature female southern kingfish collected in 2009–2010 ( $n = 833$ )

(Fig. 5). Spawning peaked earlier in 2009 (March GSI = 3.25) compared to 2010 (March GSI = 1.31). Histological analysis of gonads supported the conclusion seen with the GSI of an earlier peak spawn for 2009. Although no ovaries in final maturation or hydration were found during January and February, most fish showed evidence of oocyte development. As spring progressed, all oocyte stages were found in addition to spawning fish with POFs (Table 1). Between March–July 2009 and April–May 2010, most histological samples were classified as fully mature or ripe to spawning, with oocytes in final maturation or hydrated stages. In 2010, however, histological evidence suggested that by June, a majority of the ovaries were in the spent stage with most remaining yolking oocytes exhibiting atresia (Table 1).

Estimates of maturity for southern kingfish were derived from an examination of 637 females captured during April–August 2009 and 2010. Among those females examined, sizes ranged from 64 mm TL to 377 mm TL (mean = 237, SE =  $\pm 2.3$  mm TL) and from 2.3 to 628.8 g TW (mean = 163.3, SE =  $\pm 4.5$ ). The mean age at 50% maturity estimated by logistic regression suggested females collected between April and August matured at  $\sim 1.1$  years (Fig. 6a), and that all females were mature by age 2.

$$P(Y = 1|AGE) = \frac{e^{-17.87+16.14*AGE}}{1 + e^{-17.87+16.14*AGE}} \quad (1)$$

Histological examination confirmed that age-2 southern kingfish were fully vitellogenic with advanced yolked oocytes, suggesting spawning would occur that year. Gravid and spawning females were represented in every year class except YOY. The mean total length at 50% female maturity ( $L_{50}$ ) was 199 mm TL (Fig. 6b), and by 225 mm all females were mature.

$$P(Y = 1|TL) = \frac{e^{-20.54+0.10*TL}}{1 + e^{-20.54+0.10*TL}} \quad (2)$$

Batch fecundity of southern kingfish using the hydrated oocyte method from 36 females ranged from 22 589 oocytes for a 222 mm TL fish to 152 109 oocytes for a 324 mm TL fish.

The relationship ( $r^2 = 0.66$ ) between batch fecundity (BF) and total length (TL) was fitted with a simple exponential

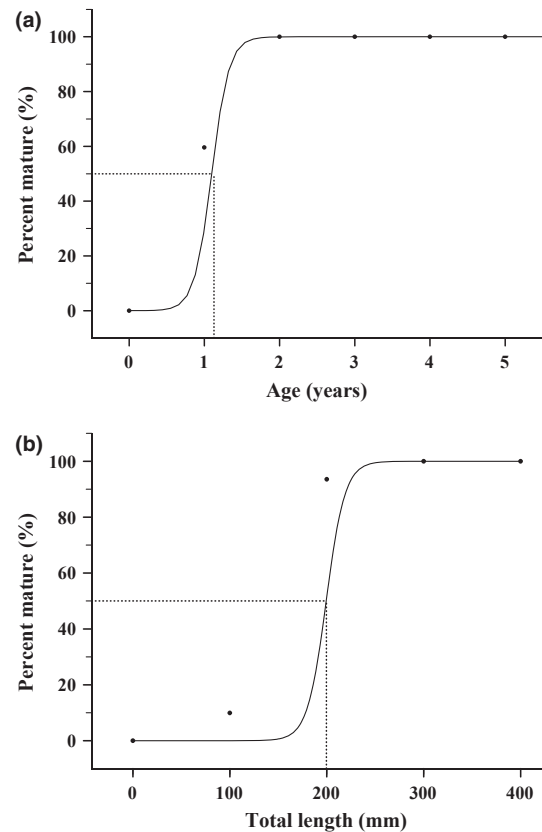


Fig. 6. Logistic regression model for the estimated percent of sexually mature female southern kingfish as a function of (a) age and (b) total length

regression in the form (Fig. 7a):

$$BF = 1307.8e^{0.0138*TL} \quad (3)$$

The relationship ( $r^2 = 0.69$ ) between BF and total weight (TW) was fitted with a simple exponential regression model in the form (Fig. 7b):

$$BF = 20,017e^{0.0044*TW} \quad (4)$$

Spawning frequency was determined by dividing the total number of mature females within the spawning season by the number of females that were hydrated or had POFs (Hunter and Macewicz, 1985; Nieland et al., 2002).

## Discussion

Prior to the current study, southern kingfish ages had only been estimated using scales (Smith and Wenner, 1985) and length-frequencies (Hildebrand and Cable, 1934; Bearden, 1963; Dahlberg, 1972; Harding and Chittenden, 1987). This study demonstrates that sectioned otoliths can be used to estimate southern kingfish ages accurately and precisely. Marginal increment analysis conclusively indicates once-yearly opaque annulus formation in sagittal otoliths is the norm for the southern kingfish ages 0–3, which covers more than 99% of the exploited age classes. The current study is the first to report accurate and precise otolith-based ages for this species, therefore useful to model population age structure and estimate rates of population growth. Otoliths should be used for age determination when

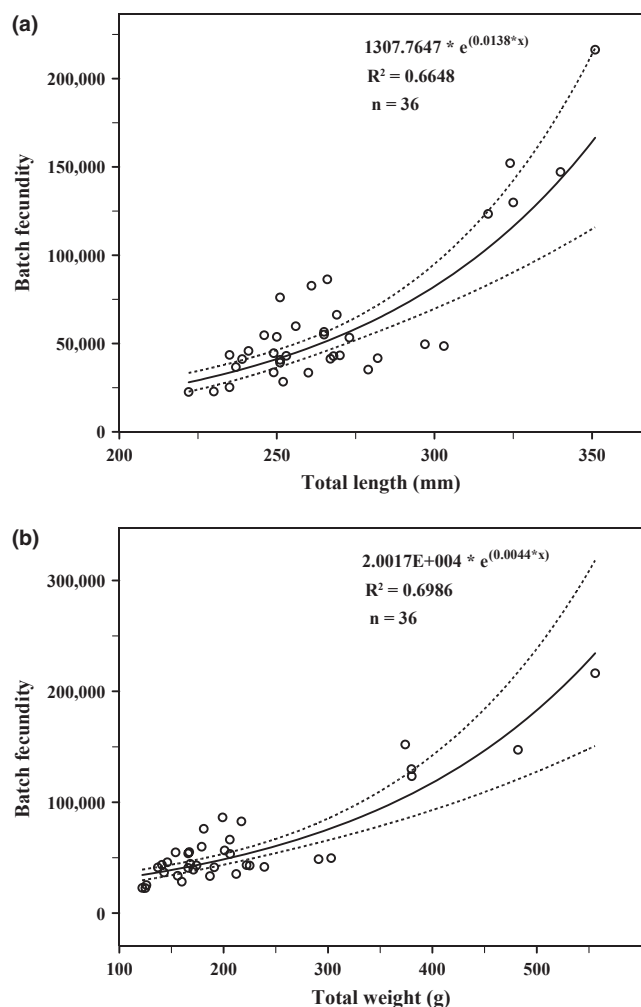


Fig. 7. Relation between southern kingfish batch fecundity and: x(a) total length; (b) total weight in Georgia for 2009–2010

more accurate description of the age structure for the species (length-at-age, length-at-maturity) is needed for resource management.

The von Bertalanffy growth model is the most popular for describing growth rates in fishes in general and among sciaenids in particular (Murphy and Taylor, 1990; Barbieri et al., 1994; Lowerre-Barbieri et al., 1994; Jones and Wells, 1998). The current study found differences in growth rates between sexes consistent with those of Smith and Wenner (1985). This difference in growth rates should be considered when estimating natural mortality, which relates directly to the productivity of the stock, the yields that can be obtained, optimal exploitation rates, management quantities, and reference points.

Based on histological analysis southern kingfish are asynchronous, batch spawners, with a continual and protracted spawning pattern. This is verified by the seasonal oocyte development patterns that define batch spawning. Previous descriptions of the spawning season for southern kingfish were April through August (Dahlberg, 1972), April to September (Hildebrand and Cable, 1934; Bearden, 1963), and April through October (Miller and Jorgensen, 1969). On the other hand, Welsh and Breder (1923) suggested southern kingfish possibly have two spawning seasons; however, the current study found no evidence of more than one spawning period. Southern king-

fish in March 2009 and April 2010 had late vitellogenic and hydrated oocytes suggesting imminent spawning. However, late vitellogenic oocytes occurred as late as August 2009 and July 2010, supporting the hypothesis of continuous spawning from spring through summer, similar to Hildebrand and Cable (1934), Bearden (1963), and Smith and Wenner (1985). Unlike previous studies, spawning seemed to cease earlier in the season, with a large proportion of females mostly recovering with primary and atretic oocytes with few advanced oocytes by September. The current study found that peak spawning occurred in April, which is earlier than other studies in the SAB: May to June in Beaufort, North Carolina (Hildebrand and Cable, 1934), June to July in South Carolina (Bearden, 1963) and June in southern and central areas of the SAB (Smith and Wenner, 1985). At a minimum, the data in this study support the variability of spawning periods in southern kingfish between years and latitude.

The current work is the first study in the SAB to report gonadosomatic index (GSI) values to describe reproductive seasonality in southern kingfish. However, GSI is not always a reliable factor on its own. By coupling GSI values with histology, this study showed that GSI did correspond with spawning peaks. Southern kingfish GSI predicted a spawning season beginning in March and ending in August for 2009, and beginning in April and ending in August for 2010. GSI of southern kingfish in the northwestern Gulf of Mexico indicate a reported spawning season from February to September (Harding and Chittenden, 1987), with a peak of March to April. In Mississippi, spawning occurred from March to September with peak spawn in April, with the GSI ranging from 0.2 to 14.5 (Fritzsch and Crowe, 1981). The peak spawning in both studies agrees with this current study with GSI data for females, showing peaks in ovarian development in March 2009 and April 2010. GSI can be used as a crude estimate of when southern kingfish might be spawning, but histology of ovaries enables more reliable indication of spawning. This is especially true if the time of onset and duration of spawning is likely to be affected by changes in the habitat. The consistency of the spawning pattern between studies could influence estimates of spawning frequency and annual fecundity because spawning effort may be variable over the spawning season as a whole (Nielsen et al., 2002).

The finding of 100% maturity among females at 225 mm TL (2 years) is quite different from the size- and age-at-maturity for female southern kingfish in South Carolina. In the current study, females 225 mm TL ranged from 178 to 188 mm SL while the other study reported age-at-maturity for southern kingfish as 2–3 years, at 230–250 mm SL. Differences in both age and ovary staging techniques might explain the discrepancy between the two studies. Bearden (1963) used length frequencies to estimate age, with some macroscopic observations of gonads to determine maturity. While the current study determined ages based on otoliths and microscopically assigned only fish with yolked oocytes as mature, making them capable of spawning that season. Harding and Chittenden (1987) reported female southern kingfish in the northwestern Gulf of Mexico matured at 150–220 mm TL in 12–14 months based on length frequencies and macroscopic assessment of gonads. Observations of the current study (50% maturity at 199 mm TL and 1.1 years) concur with these results. Age- and size-at-maturity can vary due to the energy a female has stored (Nielsen et al., 2002). If more energy is stored than is needed for growth and maintenance, then that energy can be used for reproduction

(Nieland et al., 2002). It appears that Georgia waters are conducive to female southern kingfish maturing at a smaller size than in South Carolina; however, smaller size at maturity also could be a compensatory response to heavy exploitation of southern kingfish.

Fecundity information for southern kingfish is sparse. Fritzsche and Crowe (1981) calculated total fecundity in Mississippi at 46 000–332 000 eggs (mean fecundity, 105, 349 oocytes) for 20 specimens ranging from 169 to 270 mm SL. The data in the current study revealed lower fecundity-at-size ranges in batch fecundity. Comparison of batch fecundity estimates between studies is confounded by the use of different methodologies. Fritzsche and Crowe (1981) methodology is indistinct and could have inappropriately used a determinate method: fecundity was estimated for southern kingfish from Mississippi as the standing crop of oocytes >0.30 mm in diameter which could have included oocytes not yet fully developed. The current study employed the hydrated oocyte method (Hunter and Macewicz, 1985), which is believed to be the most credible and dependable means of batch fecundity estimation. The estimates of batch fecundity-at-size showed less variability than Fritzsche and Crowe (1981), for the size range of spawners sampled. The methodology of the previous study could have under-estimated total fecundity for this species. If batch size changes over the spawning season or inter-annually, any relationship between fecundity and size based on the entire season will be highly variable, confounding the simple calculations that we made. Nevertheless, the current study is able to resolve the proportion of spawning effort in Georgia and the total annual fecundity.

Among 183 mature females collected during the March–August 2009–2010 spawning seasons in Georgia, 42% were spawning in March 2009 and 56% in April 2010. Spawning frequencies estimated from the proportion of mature females with hydrated oocytes were 2 day in 2009 and 4.2 day in 2010. Given spawning frequencies of 2 or 4.2 day and a 180 day spawning season, southern kingfish in Georgia spawned between 43 and 89 times during each spawning season and may be expected to spawn, on average, 2.9–6 million ova per season. These numbers are similar to previous studies that suggest spotted seatrout, a sciaenid of greater size and longer life span, may spawn 9–11 million ova (Nieland et al., 2002) over a comparable spawning season.

In summary, the study indicates southern kingfish ages using sectioned otoliths are accurate with a high degree of precision. Differences in growth rates between sexes were found. The current study found that southern kingfish are asynchronous, batch spawners, with a continual and protracted spawning pattern. Coupling GSI values with histology reveals a spawning season from March through August with peak activity in April. Southern kingfish are multiple spawners capable of spawning every 2.0–4.2 days and producing 2.9–6 million ova per season.

### Acknowledgements

The authors would like to thank Dr. Matthew Gilligan and Dr. Mary Carla Curran for their service, time, and assistance. Logistical support was provided by the Georgia Department of Natural Resources, C. Belcher, J. Boles, D. Franco, M. Hinman, S. Kicklighter, T. Mathes, J. Page, B. Readdick, D. Roberson, and K. Wolfe; Savannah State University, Capt. J. Rosenzweig; University of Georgia R/V Bulldog; Sea Island Company, Capt. C. Fordham, and for

all whom helped with the collection and processing of samples in the study. Thank you to L. Cammon of the Sapelo Island Institute Library who helped provide reference papers. Finally, big thanks to C. Belcher, K. Knowlton, M. Wuenschel and P. Geer for taking the time to read and give suggestions on this manuscript.

### References

- Bagenal, T. B.; Tesch, F. W., 1978: Age and growth. In: Methods for assessment of fish production in fresh waters. pp. 101–136. T. B. Bagenal (Ed.). Blackwell Scientific Publications, Oxford, pp. 365.
- Barbieri, L. R.; Chittenden, M. E., Jr; Jones, C. M., 1994: Age, growth, and mortality of Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay region, with a discussion of apparent geographic changes in population dynamics. Fish. Bull. **92**, 1–12.
- Beamish, R. J.; McFarlane, G. A., 1983: The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Soc. **112**, 735–743.
- Bearden, C. M., 1963: A contribution to the biology of the king whittings, genus *Menticirrhus*, of South Carolina. Contrib. Bears Bluff Lab. **38**, pp. 27.
- Campana, S. E., 2001: Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. **59**, 197–242.
- Campana, S. E.; Jones, C. M., 1992: Analysis of otolith microstructure data. In: Otolith microstructure examination and analysis. D. K. Stevenson, S. E. Campana (Eds). Can. Spec. Publ. Fish. Aquat. Sci. **117**, 73–100.
- Campana, S. E.; Nielson, J. D., 1985: Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. **42**, 1014–1032.
- Chang, W. Y. B., 1982: A statistical method for evaluating the reproducibility of age determination. Can. J. Fish. Aquat. Sci. **39**, 1208–1210.
- Dahlberg, M. D., 1972: An ecological study of Georgia coastal fishes. Fish. Bull. **70**, 323–353.
- Fritzsche, R. A.; Crowe, B. J., 1981: Contributions to the life history of the southern kingfish, *Menticirrhus americanus* (Linnaeus), in Mississippi. Mississippi Department of Wildlife Conservation, Bureau of Marine Resources, Long Beach.
- Harding, S. M.; Chittenden, M. E., Jr, 1987: Reproduction, movements, and population dynamics of the southern kingfish, *Menticirrhus americanus*, in the northwestern Gulf of Mexico. NOAA Tech. Rep. NMFS **49**, 1–21.
- Hildebrand, S. F.; Cable, L. E., 1934: Reproduction and development of whittings or kingfishes, drums, spot, croaker, and weakfishes or seatrouts, family Sciaenidae off the Atlantic coast of the United States. Fish. Bull. **43**, 1–388.
- Hoenig, J. M.; Morgan, M. J.; Brown, C. M., 1995: Analyzing differences between two age determination methods by tests of symmetry. Can. J. Fish. Aquat. Sci. **52**, 364–368.
- Hunter, J. R.; Macewicz, B. J., 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.). NOAA Tech. Rep. NMFS **36**, 79–94.
- Hunter, J. R.; Lo, N. C. H.; Leong, R. J. H., 1985: Batch fecundity 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.). NOAA Tech. Rep. NMFS **36**, 67–77.
- Jones, C. M.; Wells, B., 1998: Age, growth, and mortality of black drum, *Pogonias cromis*, in the Chesapeake Bay region. Fish. Bull. **96**, 451–461.
- Kimura, D. K., 1980: Likelihood methods for the von Bertalanffy growth curve. Fish. Bull. **77**, 765–776.
- Lowerre-Barbieri, S. K.; Chittenden, M. E., Jr; Jones, C. M., 1994: A comparison of a validated otolith method to age weakfish, *Cynoscion regalis*, with the traditional scale method. Fish. Bull. **92**, 555–568.
- Luna, L. G., 1968: Manual of histological staining methods of the Armed Forces Institute of Pathology. McGraw Hill, New York, pp. 258.

- Miller, J. M.; Jorgensen, S. C., 1969: Seasonal abundance and length frequency distribution of some marine fishes in coastal Georgia. U.S. Fish Wildl. Serv. Data Rep. **35**, pp. 102.
- Murphy, M. D.; Taylor, R. G., 1990: Reproduction, growth, and mortality of red drum *Sciaenops ocellatus* in Florida waters. Fish. Bull. **88**, 531–542.
- Nieland, D. L.; Thomas, R. G.; Wilson, C. A., 2002: Age, growth, and reproduction of spotted seatrout in Barataria Bay, Louisiana. Trans. Am. Fish. Soc. **131**, 245–259.
- Ricker, W. E., 1975: Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. **191**, 382.
- Robillard, E.; Reiss, C. S.; Jones, C. M., 2008: Reproductive biology of bluefish (*Pomatomus saltatrix*) along the East Coast of United States. Fish. Res. **90**, 198–208.
- Schaefer, R. H., 1965: Age and growth of the northern kingfish in New York waters. NY Fish Game J. **12**, 191–216.
- Sikora, W. B.; Sikora, J. P., 1982: Habitat suitability index models: southern kingfish. U.S. Dept. Fish Wildl. Serv. FWS/OBS-82/10.31, pp. 22.
- Smith, J. W.; Wenner, C. A., 1985: Biology of the southern kingfish in the South Atlantic Bight. Trans. Am. Fish. Soc. **114**, 356–366.
- S-Plus, 2001: S-Plus 6.1 for windows guide to statistics. Insightful Corp., Seattle.
- Welsh, W. W.; Breder, C. M., 1923: Contributions to the life histories of Sciaenidae of the eastern United States coast. Bull. US Bur. Fish. **39**, 141–201.
- West, G., 1990: Methods of assessing ovarian development in fishes: a review. Aus. J. Mar. Freshwat. Res. **41**, 199–222.
- Wilson, D. C., 2000: Bluefish science in the northeast region: a case study, vol. 48. Institute for Fisheries Management and Coastal Community Development. Institute for Fisheries Management North Sea Center, Hirtshals, pp. 39.
- Author's address:** Donna E. McDowell, Georgia Department of Natural Resources, Coastal Resources Division, One Conservation Way, Brunswick, GA 31520, USA.  
E-mail: Donna.McDowell@dnr.state.ga.us