Age, Growth, and Reproduction of Sheepsheads in South Carolina

Authors: McDonough, C. J., Wenner, C. A., and Roumillat, W. A.

Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 3(1) : 366-382

Published By: American Fisheries Society

URL: https://doi.org/10.1080/19425120.2011.632234

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 27 Dec 2024
Terms of Use: https://bioone.org/terms-of-use

Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 3:366–382, 2011
© American Fisheries Society 2011
ISSN: 1942-5120 online
DOI: 10.1080/19425120.2011.632234

ARTICLE

Age, Growth, and Reproduction of Sheepsheads in South Carolina

C. J. McDonough,* C. A. Wenner, and W. A. Roumillat
South Carolina Department of Natural Resources, Marine Resources Research Institute,
217 Fort Johnson Road, Charleston, South Carolina 29412, USA

Abstract

The sheepshead *Archosargus probatocephalus* is a common estuarine and reef species that is found year round in South Carolina. Although not commercially important, the sheepshead is a significant recreational species, and most of the fishing pressure occurs in state waters. From 1990 to 2005, 5,692 sheepsheads were collected from fishery-dependent and fishery-independent monitoring programs in South Carolina. Fish ranged from 102 to 605 mm in fork length (FL) and were caught during every month of the year. Ages ranged from 0 to 19 years for males and from 0 to 23 years for females; the dominant age-classes were ages 2–5. Marginal increment analysis confirmed the formation of a single annulus per year, and annulus formation began in May. Males and females did not significantly differ in FL at age t(FL_t) or total weight at age t (W_t); the pooled von Bertalanffy growth models were $FL_t = 498[1 - e^{-0.297(t + 1.10)}]$ and $W_t = 3{,}778[1 - e^{-0.165(t - 0.548)}]^{2.997}$. Both males and females exhibited the first signs of sexual maturity at age 1, and 100% maturity was reached at age 4. Batch fecundity estimated late in the spawning season ranged from 18,400 to 738,500 oocytes/spawning event and averaged 235,000 oocytes/spawning event. Fork length, *W*, and age were positively correlated with fecundity. Although size was a better predictor of fecundity than age, the relationship was weak due to the high variability in size at age. Comparisons of growth parameters for sheepsheads studied in the southeastern United States indicated that South Carolina sheepsheads tend to have a larger maximum FL and a greater maximum age than fish found in the Gulf of Mexico.

The sheepshead *Archosargus probatocephalus* is a common marine and estuarine sparid (Pisces: Sparidae) found from Nova Scotia to Brazil in the western Atlantic Ocean (Caldwell 1965). Two subspecies of sheepshead—*A. probatocephalus probatocephalus* and *A. probatocephalus oviceps*—have been described in the Gulf of Mexico and Caribbean based on morphometrics and color banding patterns (Caldwell 1965); however, recent work has determined that these subspecies are not readily distinguishable genetically in the Gulf of Mexico (Anderson et al. 2008). Only *A. probatocephalus probatocephalus* has been identified in South Carolina. Sheepsheads generally spawn at nearshore reef sites in late winter and early spring along the mid- and south Atlantic coasts of the United States (Jennings 1985), although there is evidence of estuarine spawning in the Gulf of Mexico (Render and Wilson 1992). The pelagic juvenile stage lasts 30–40 d and is followed by recruitment to estuarine intertidal marsh grass and mudflat habitats (Springer and Woodburn 1960; Odum and Heald 1972; Parsons and Peters 1987; Tucker and Alshuth 1997; Lehnert and Allen 2002). Once juveniles reach approximately 40 mm fork length (FL), they move to high-relief bottom structure, such as oyster bars, jetties, sea walls, and piers, and can often be found in low-salinity brackish zones (Johnson 1978).

Although sheepsheads are reported as a commercial species in South Carolina, they are not targeted by commercial fisheries and historically have been considered as bycatch in commercial shrimp trawling or offshore longlining operations (NMFS 2006). From 1981 to 2004, the reported commercial landings of

---

Subject editor: Debra J. Murie, University of Florida, Gainesville

*Corresponding author: mcdonoughc@dnr.sc.gov
Received May 24, 2010; accepted July 26, 2011

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 27 Dec 2024
Terms of Use: https://bioone.org/terms-of-use

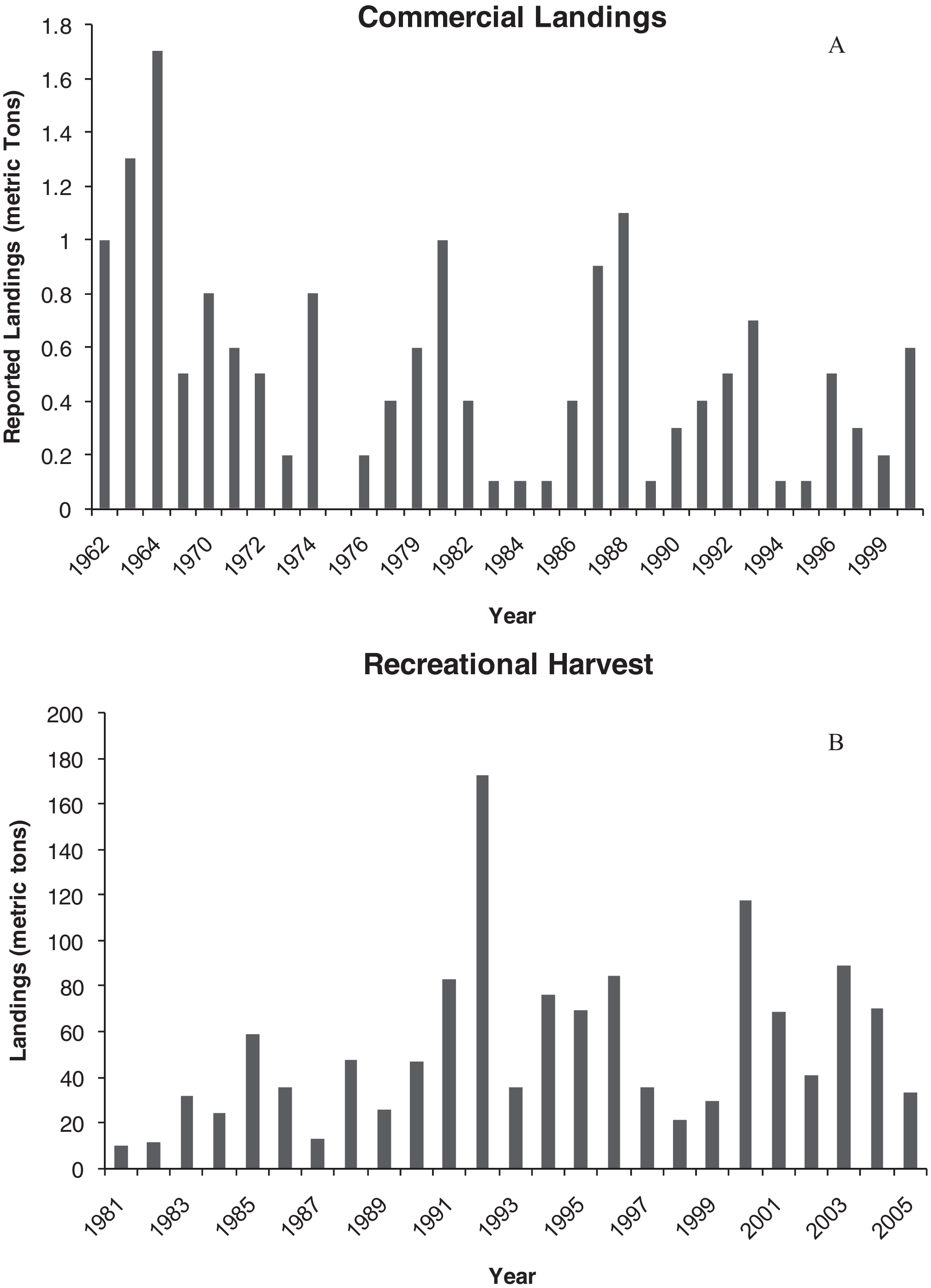

FIGURE 1. Fishery landings of sheepsheads in South Carolina: **(A)** commercial landings (1961–2005) and **(B)** recreational harvest (1981–2005; A + B1, where A = fish kept and B1 = discards; data source: NMFS 2006).

sheepsheads in South Carolina totaled 8.4 metric tons. This total was similar to Georgia's sheepshead catch (9.9 metric tons) but was several orders of magnitude lower than the catch in North Carolina (444.8 metric tons) and along the east coast of Florida (2,550.8 metric tons; NMFS 2006). The higher commercial landings in both North Carolina and Florida were due to commercial fisheries that targeted sheepsheads. South Carolina's catch of sheepsheads made up only 0.28% of the total commercial landings for the southeastern U.S. Atlantic coast during 1981–2005. Year-to-year catches have been highly variable, and there has been no discernible long-term trend in the landings since the 1960s (Figure 1A). In South Carolina and the other

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 27 Dec 2024
Terms of Use: https://bioone.org/terms-of-use

southeastern states, the recreational landings of sheepsheads are much higher than commercial landings. For the entire southeastern U.S. coast, the east coast of Florida accounted for the majority (66.8%) of the recreational catch of sheepsheads, followed by South Carolina (14.5%), North Carolina (9.5%), and then Georgia (9.1%). The total recreational catch of sheepsheads in South Carolina for 1981–2007 (2,500 metric tons) was significantly higher than the commercial landings (6.9 metric tons). The Marine Recreational Fisheries Statistics Survey (MRFSS; NMFS 2006) landings data from South Carolina demonstrated peaks in sheepshead catch approximately every 4 years, but these were not related to peaks in the commercial catch (Figure 1B). The total number of angler trips per year was variable but increased significantly during 1981–2005 (increase = 71.5% since the early 1980s).

Despite the economic importance of sheepsheads, information concerning the biology of this species along the southeastern U.S. Atlantic coast is lacking. Two important components of the analysis of a fish population are (1) an adequate representation of the size structure and age structure of the population and (2) identification of the size and age at which the fish reach sexual maturity, coupled with assessment of general reproductive output (fecundity). Ages based on the examination of scales have been reported for sheepsheads in North Carolina (Schwartz 1990) and Georgia (Music and Pafford 1984), but the use of scales for aging is difficult in long-lived fishes because growth slows appreciably as the fish approach maximum sizes, thus causing scale annuli to become crowded and increasingly difficult to read (Boehlert 1985). Additional problems with scale-based age determination include scale regeneration, presence of anomalous check marks, and reabsorption of calcium (Secor et al. 1995). Ages derived from scales tend to underestimate the maximum fish age in a population (Boehlert 1985). The use of otoliths has been shown to be more accurate than the use of scales and is a validated aging method for sheepsheads from the Gulf of Mexico (Beckman et al. 1991; Dutka-Gianelli and Murie 2001). To date, however, no studies have corroborated the use of otoliths for determining age in sheepsheads along the southeastern U.S. Atlantic coast. Size and age at sexual maturity are also important because they allow for the implementation of management strategies that reduce fishing pressure on juveniles and subadults, thereby facilitating escapement to increase spawning biomass.

Sheepsheads have been managed as a federally regulated species in South Carolina because they spawn at offshore reef sites in both federal (>5.556 km [3 nautical miles] offshore) and state (<5.556 km offshore) waters. Currently, there are no size restrictions for sheepsheads in South Carolina, and the established bag limit is 20 fish·person^{-1}·d^{-1} in aggregate with species belonging to the snapper–grouper complex. Future management actions related to the sheepshead are limited by a lack of data needed for stock assessment. Since sheepsheads are found in abundance inshore as well as offshore, they may be more susceptible to overfishing than the other species included in the snapper–grouper management plan (NMFS 2006).

The objectives of this study were to (1) use marginal increment analysis (MIA) to validate the use of otoliths for determining the age of sheepsheads from South Carolina, (2) examine growth of male and female sheepsheads by using von Bertalanffy growth models, (3) determine the size and age at maturity for males and females, and (4) estimate batch fecundity in relation to female size for sheepsheads from South Carolina.

METHODS

Fish collections.—Sheepsheads were collected from both fishery-dependent and fishery-independent sources over a 15-year period (1990–2005) from inshore, nearshore, and offshore waters of South Carolina (Figure 2). The fishery-dependent samples (hook and line) were from two sources: fishing tournaments and angler donations to the South Carolina Department of Natural Resources' (SCDNR) fish "wrack" recycling program (i.e., frozen carcasses of filleted fish; Wenner and Archambault 2006). The fishery-independent samples were obtained by the SCDNR during three different monitoring programs, including a stop-net program, a trammel-net program, and an electrofishing program. The stop-net program was conducted from 1985 to 1994 and used fixed index sampling sites that were sampled monthly (Figure 2). The purpose of the stop-net program was to monitor important recreational finfish species in order to establish population size structure, age structure, seasonality, reproductive dynamics, and overall abundance. The trammel-net survey has been conducted since 1991 and is currently ongoing. This program uses a stratified random sampling protocol in seven different estuaries (i.e., strata; Figure 2); individual sampling sites are chosen at random within each estuarine area on a monthly basis. The trammel-net program was designed to monitor important recreational finfish species over a broader geographic range than the stop-net program, and the stratified random design was more statistically robust. The electroshock sampling program began in 2001 and is also currently ongoing. The electroshock program also uses a monthly stratified random sampling design with six estuaries serving as strata (Figure 2). The electroshock boat survey was designed to complement the trammel-net survey by sampling the low-salinity brackish and tidal freshwater portions of estuaries where the trammel nets had already sampled but could not be used effectively.

Fish that were caught during the fishery-independent surveys were measured for total length (TL), FL, and standard length (SL) and were released alive. A small number of specimens (n = 40) that suffered capture mortality during the fishery-independent surveys were retained for determinations of sex, maturity, and age. Fish that were sampled by fishery-dependent methods were similarly measured for length and total weight (W; tournament samples only); their sex and maturity status were assessed, and otolith samples were collected for age determination.

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 27 Dec 2024
Terms of Use: https://bioone.org/terms-of-use

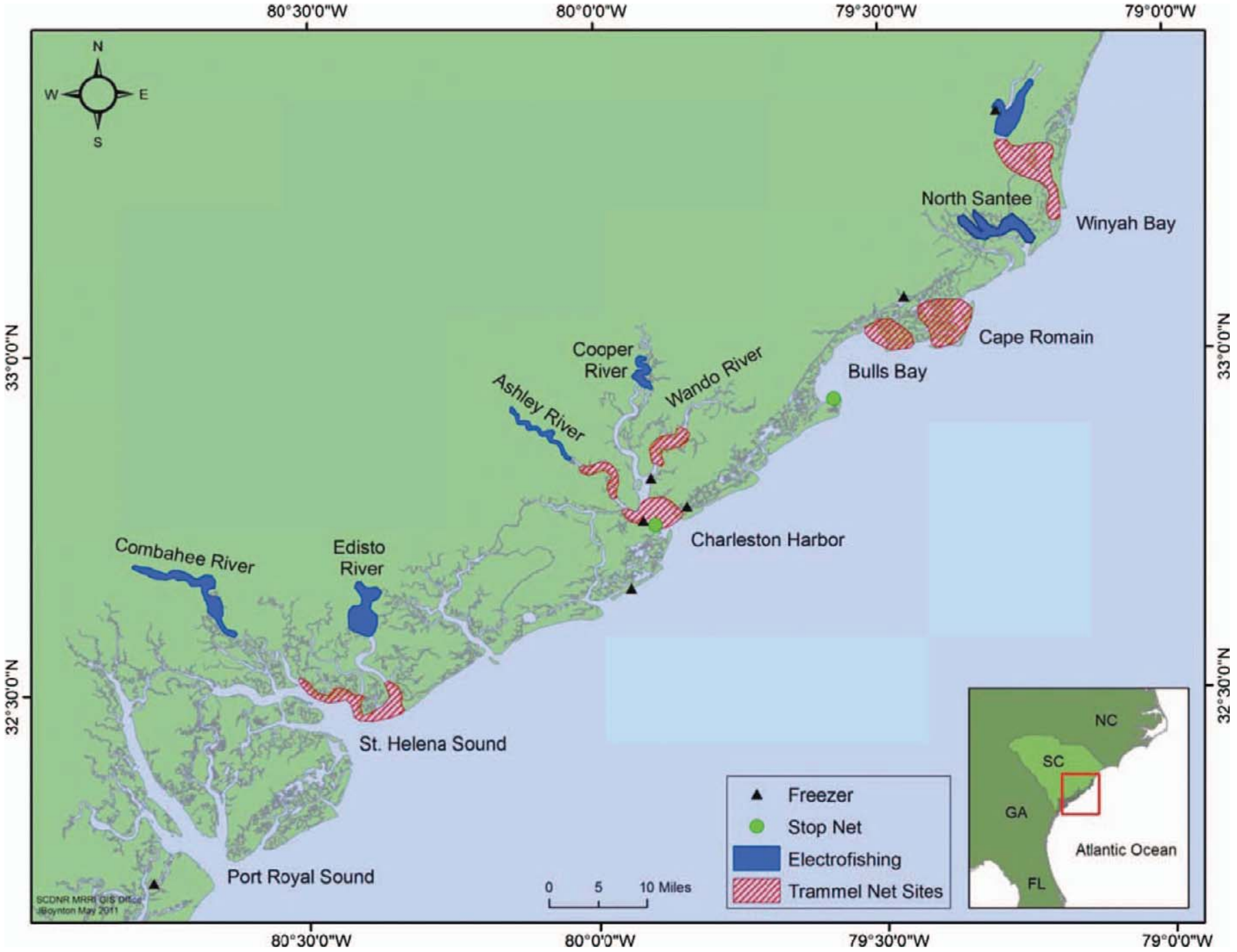

FIGURE 2. Estuarine sampling strata for stop-net, trammel-net, and electroshock boat surveys of sheepsheads in South Carolina and locations of freezers for the recreational fish wrack recycling program. Fish that were donated to the fish wrack recycling program were generally captured within a 16.093-km (10-mi) radius of the freezer location.

Aging and validation.—Age was determined for a total of 2,881 fish, 98.6% of which were either fishing tournament or fish wrack specimens (i.e., angler captures). The remaining fish came from the trammel-net (0.9%) or stop-net (0.5%) survey. Age was determined by using the left sagittal otolith, which was embedded in epoxy resin. A 0.5-mm transverse section encompassing the otolith core was cut by using a low-speed Isomet saw with diamond wafering blades and was mounted on a microscope slide. The section was viewed with a dissecting microscope at 50× magnification, and initial age was recorded as the number of annuli present. Ages were then adjusted based on the date of capture and a presumed birth date of 1 May, which took into account when annuli were laid down (May–June) and when the spawning season ended (see Results). The end of the spawning season (early May) and the deposition of annuli both occurred during the same time period; thus, the assigned age would closely approximate the absolute age. Annuli were most legible along the sulcal groove of sectioned otoliths (Figure 3).

All otoliths were blind evaluated by two readers. Age data recorded by the two readers were compared to determine the percentage of otolith age readings that agreed exactly or that agreed within 1 year (Campana et al. 1995). Otoliths for which there was a disagreement between readings were reevaluated simultaneously by both readers and were discarded if a consensus could not be reached. Ages were compared between the two readers by using a paired *t*-test and Wilcoxon's signed rank test, and the coefficient of variation ([SD/mean] × 100) was also used to compare the two data sets (Chang 1982; Hoenig et al. 1995).

Marginal increments (defined as the distance between the opaque zone of the last visible annulus and the edge of the otolith) were measured for 1–5-year-old fish in order to establish the timing and periodicity of increment deposition.

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 27 Dec 2024
Terms of Use: https://bioone.org/terms-of-use

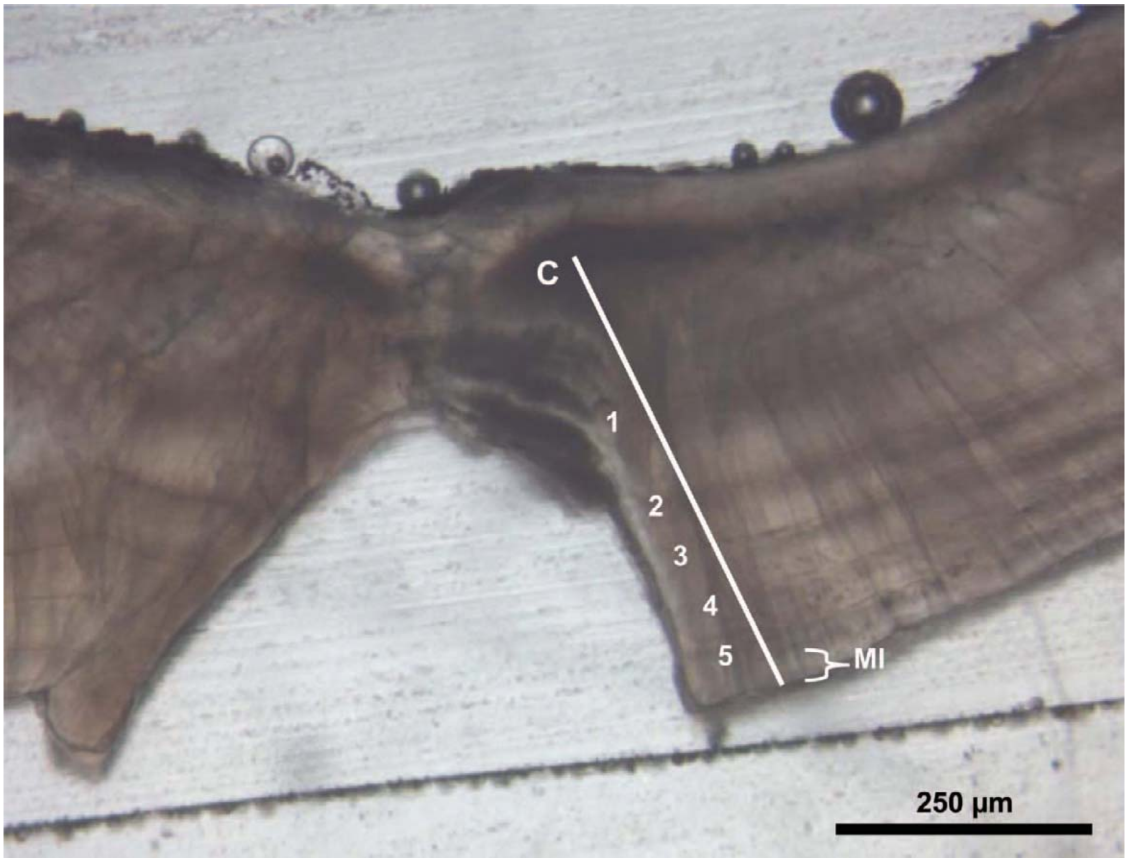

FIGURE 3. Photomicrograph of an otolith from a 5-year-old sheepshead; the otolith was cross-sectioned through the core (C), annuli are indicated by number, and the marginal increment (MI) is marked.

Increment widths were only measured for ages 1–5 because the natural decrease in annulus widths was difficult to measure in older fish (i.e., natural growth slowed as individuals approached asymptotic lengths [L_∞]; Campana 2001). Marginal increment analysis was performed for each age-group separately and for the pooled data to validate timing of annulus deposition. Periodicity of annulus deposition was determined by examining marginal increment widths for the period 2000–2002 to confirm that increments were deposited annually.

Growth.—There were no published values for sheepshead length conversions between TL, FL, and SL, so conversion factors were calculated by using linear regressions to allow for comparisons with previous studies. Significant differences between males and females for any of the length measurement conversions (TL, FL, and SL) were tested with analysis of covariance.

The relationship between W and FL was examined by using a nonlinear regression,

$$W = a(\text{FL})^b,$$

where a is the y-intercept and b is the regression coefficient (slope). The difference in this relationship (based on log-transformed FL and W) between sexes was tested by use of a general linear model with sex as a categorical factor and weight as a covariate (Zar 1984).

The relationship between FL and age was described by the von Bertalanffy growth equation applied separately to males and females:

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

where FL_t is the FL at age t; k is the growth coefficient; and t_0 is the hypothetical age at a FL of zero. The von Bertalanffy growth model parameters were also estimated by using W as a function of age (Beverton and Holt 1957; Beckman et al. 1991):

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

where W_t is weight at age t; W_∞ is asymptotic weight; $t_0 =$ hypothetical age at a weight of zero; and $b =$ slope value from the regression equation describing W as a function of FL.

Differences in growth between male and female sheepsheads were examined with a variance ratio test (Zar 1984; Dutka-Gianelli and Murie 2001). If there was no significant difference

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 27 Dec 2024
Terms of Use: https://bioone.org/terms-of-use

between the sexes, the data were combined into a single growth model.

Maturity and fecundity.—Initial sex and maturity information was determined through gross visual examination of all dead fish collected and was assessed based on the macroscopic morphological criteria presented by Brown-Peterson et al. (2011). For histological confirmation of maturity, a sample of gonad tissue was removed from sacrificed fish that had not been frozen (mostly fish that were captured during tournaments). Tissues were processed by using standard methodology for histological paraffin embedding and hematoxylin and eosin-y staining (Humason 1967). For histological sections, maturity was assigned according to Brown-Peterson et al. (2011) and included five basic stages: immature, developing, spawning capable, regressing (spent), and regenerating (resting). The latter four stages were all considered to represent sexually mature fish. The spawning-capable stage applies to fish that are developmentally and physiologically able to spawn within a given cycle or season, but the actual oocyte developmental stage can range from different vitellogenic stages through the fully hydrated and ripe oocyte stages (i.e., indicating that spawning is imminent). In batch-spawning fishes, this process can occur multiple times during a spawning season as each new batch of oocytes develops before recruiting for the next spawning event. The proportion of mature sheepsheads in each size-class (10-mm FL bins) and age-class was examined by using a logistic regression, $Z = a + b(\mathrm{FL\ or\ age})$, where Z is the logistic regression Z-function value, a is the y-intercept, and b is the regression coefficient. Logistic regression of maturity at size and age was modeled for both sexes combined by using sex as a factor or was modeled with the sexes pooled if there was no significant difference. The maturity probability was determined by using the equation

$$p_{\mathrm{maturity}} = \frac{e^{z}}{1 + e^{-z}},$$

where p_{maturity} is the probability of maturity at a given size or age and Z is the estimate from the logistic regression.

Spawning-capable female sheepsheads with either fully hydrated oocytes or oocytes that were undergoing final maturation were collected from spring recreational fishing tournaments held during April from 2001 to 2006, and these fish were used to determine batch fecundity relative to length, weight, and age. Fecundity was determined by using the gravimetric method described by Roumillat and Brouwer (2004). Spawning frequency was estimated by use of the postovulatory follicle (POF) method (Hunter and Macewicz 1985). The presence of POFs indicates that spawning has occurred within the previous 48 h (Hunter and Macewicz 1985; Fitzhugh and Hettler 1995; Roumillat and Brouwer 2004); POFs were commonly observed in sheepsheads collected during April and early May. Postovulatory follicles were observed during the spawning-capable stage, when a new batch of oocytes was recruiting for the next spawning event.

RESULTS

Fish Collections

Four different gear types accounted for 97.2% of the total sheepshead catch ($n = 5{,}692$) obtained during 1990–2005. Most (64.3% of total catch) were caught with hook and line from recreational fishing tournaments (31.7% of total catch) or from the SCDNR fish wrack recycling program (32.6% of total catch). The majority of samples were obtained from inshore waters, whereas only a small number of samples (5.9% of total catch) came from offshore reef sites. The remaining specimens were captured in SCDNR fishery-independent monitoring programs, which included trammel nets (20.5% of total catch), stop nets (10.7% of total catch), juvenile fish surveys (2.8%), and electroshock boats (1.7% of total catch).

Sheepsheads were caught during every month of the year, although the summer (June–August) and fall (September–November) months accounted for the majority (70.4%) of catch obtained over the entire time period. Sheepsheads ranged in size from 102 to 605 mm FL (Figure 4); the overall mean ± SD was 368 ± 77.9 mm FL. Kolmogorov–Smirnov two-sample tests comparing the different groups indicated that the mean FL of sheepsheads from tournaments (mean ± SD = 392.5 ± 76.7 mm) differed significantly from the mean FL of specimens from the fish wrack recycling program (350.3 ± 79.0 mm; $P < 0.001$) and the trammel-net survey (341.6 ± 114.5 mm; $P < 0.001$); the mean FLs of fish from the trammel-net survey and fish wrack program were also significantly different ($P < 0.001$). The difference was attributable to the fact that almost all of the specimens smaller than 200 mm FL (138 of 142 fish) were captured in trammel nets, resulting in much higher variances for this data set.

Aging and Validation

Otoliths used for aging were removed from 2,881 sheepsheads. Of these, 39.5% of the fish were from fishing tournaments and 59.1% were from the fish wrack recycling program; the remaining fish were from the trammel-net (0.9%) and stop-net (0.5%) surveys. Sheepshead ages ranged from 0 to 23 years; 73.5% of the specimens were ages 2–5. A Kolmogorov–Smirnov test comparing the age distributions between the different data sources indicated significant differences ($P < 0.001$) between the fish wrack and tournament specimens, whereas the stop-net and trammel-net distributions were not significantly different ($P = 0.082$; Figure 5). Age ranged from 0 to 19 years for males and from 0 to 23 years for females.

Annulus counts by the two readers were in exact agreement for 82.8% of specimens and agreed within 1 year for 98.3% of specimens. The paired t-test ($P = 0.418$) and Wilcoxon's signed rank test ($P = 0.418$) indicated no significant difference between otolith age assignments made by the two readers, and the coefficient of variation was low (0.034).

The smallest mean marginal increment occurred each year in July and August, and annuli were deposited yearly (Figure 6A).

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 27 Dec 2024
Terms of Use: https://bioone.org/terms-of-use

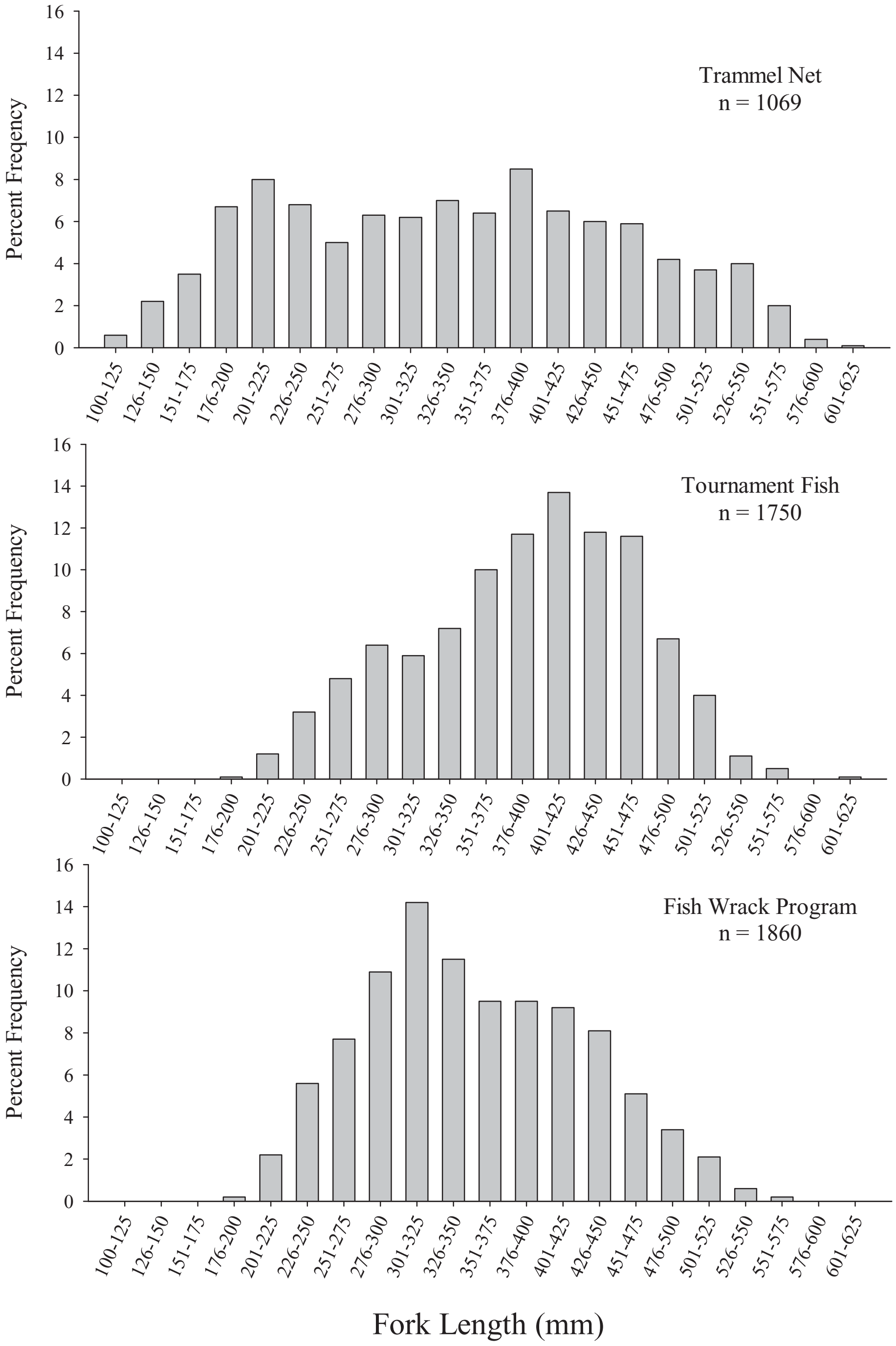

FIGURE 4. Size frequency distributions of sheepsheads sampled in South Carolina estuaries from 1990 to 2005; fish were collected by trammel-net surveys, tournaments, and a recreational fish wrack recycling program.

Deposition of the first annulus near the edge of otoliths initially occurred in May or June, and fish of ages 1–5 showed similar patterns of monthly increment deposition (Figure 6B).

Growth

There was no significant difference between males and females for any of the length conversions (TL to FL: $P = 0.116$; TL to SL: $P = 0.891$; SL to FL: $P = 0.653$), and therefore the sexes were pooled:

$$\mathrm{FL} = 1.22 + 0.930(\mathrm{TL}),$$

$$\mathrm{SL} = -6.55 + 0.799(\mathrm{TL}),$$

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 27 Dec 2024
Terms of Use: https://bioone.org/terms-of-use

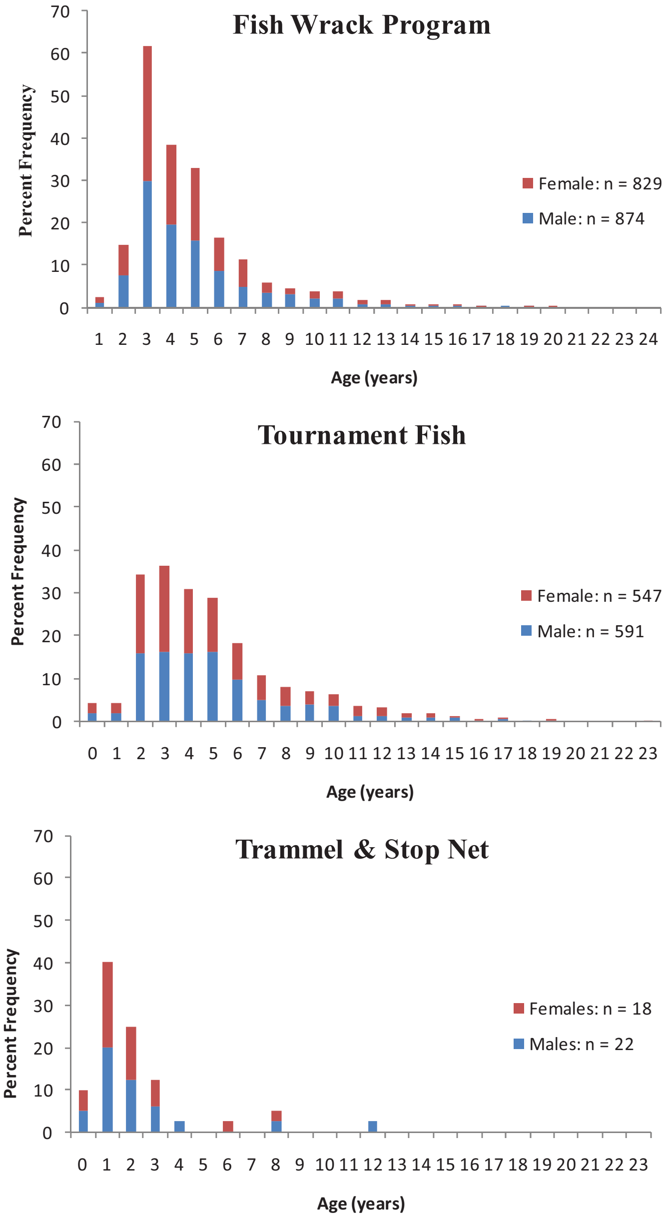

FIGURE 5. Age frequency distributions of male and female sheepsheads sampled in South Carolina estuaries from 1990 to 2005; fish were collected by a recreational fish wrack recycling program, tournaments, and trammel-net and stop-net surveys.

and

$$\mathrm{FL} = 9.36 + 1.120(\mathrm{SL})$$

(TL to FL: $r^2 = 0.998$, df = 3,707; TL to SL: $r^2 = 0.996$, df = 3,702; SL to FL: $r^2 = 0.997$, df = 3,714). The general linear model showed no significant difference between sexes in W as a function of FL ($P = 0.696$), so the sexes were pooled in a combined W–FL regression (Figure 7),

$$W = (5.47 \times 10^{-5})\mathrm{FL}^{2.997}.$$

There was no significant difference in von Bertalanffy growth models between males and females for FL as a function of age (variance ratio test: $F = 0.231$, $P = 0.631$), and thus the sexes were combined to produce an overall growth model:

$$\mathrm{FL}_t = 498\left[1 - e^{-0.297(t+1.10)}\right]$$

($r^2 = 0.763$, $P < 0.001$, $n = 2{,}705$; Figure 8, upper panel). There was also no significant difference between males and females in W as a function of age (variance ratio test: $F = 1.01$, $P = 0.11$), and the data were therefore pooled:

$$W_t = 3{,}778\left[1 - e^{-0.165(t-0.548)}\right]^{2.997}$$

($r^2 = 0.843$, $n = 1{,}129$; Figure 8, lower panel).

Maturity and Fecundity

The sex ratios between hook-and-line gear and trammel-net gear were not different from 1:1 (chi-square value [χ^2] = 0.011, $P = 0.917$). Sexually immature sheepsheads were observed in collections during April–December but were not present in collections made during January–March. Offshore reef specimens were mostly collected during January–May, and 92.3% of those fish were undergoing some stage of reproductive development. Regenerating or resting (sexually mature but reproductively inactive) adults were found to occur year round but were far less frequent from January to April (Figure 9). Histological sections from females indicated the occurrence of all stages of oocyte development (primary growth oocytes, cortical alveolar oocytes, vitellogenic oocytes, and final oocyte maturation; Wenner et al. 1986; Brown-Peterson et al. 2011) during March and April (Figure 10). The presence of multiple oocyte developmental stages was indicative of asynchronous or batch-spawning behavior. Developing females were observed to contain POFs in April and early May, indicating recent spawning activity, but POFs were not seen after these months. Fully spawning-capable or ripe (hydrated) females were observed mostly in samples collected during April and the beginning of May. Ovaries in the spawning-capable stage were evident during February and March in the fish wrack specimens, but histological confirmation of this stage (and of POFs) was impossible because of cellular degradation from the preservation method (freezing) used by this survey. Atrophy of both ovaries and testes was found during February–June, and spawning activity ceased by the middle of May. Given that (1) the majority of mature females did not show oocyte development stages indicative of active spawning until February and (2) POFs were not observed in histological sections after mid-May, the conservative estimate of the spawning season for sheepsheads in South Carolina would be February through mid-May.

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 27 Dec 2024
Terms of Use: https://bioone.org/terms-of-use

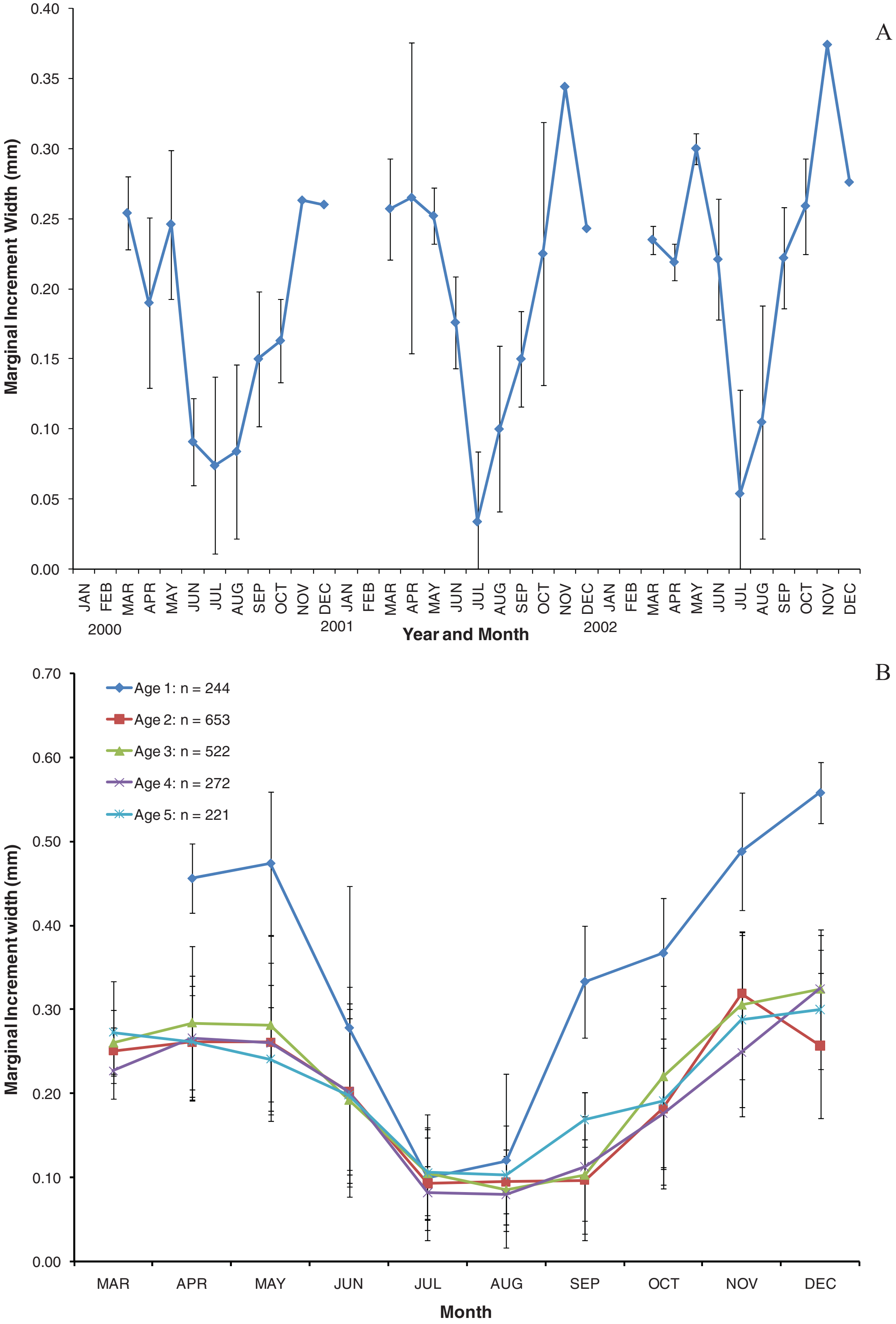

FIGURE 6. Mean (± SD) marginal increment widths in otoliths of sheepsheads sampled from South Carolina estuaries: **(A)** ages 1–5 combined (presented by month from 2000 to 2002); and **(B)** individual age-classes (presented by month).

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 27 Dec 2024
Terms of Use: https://bioone.org/terms-of-use

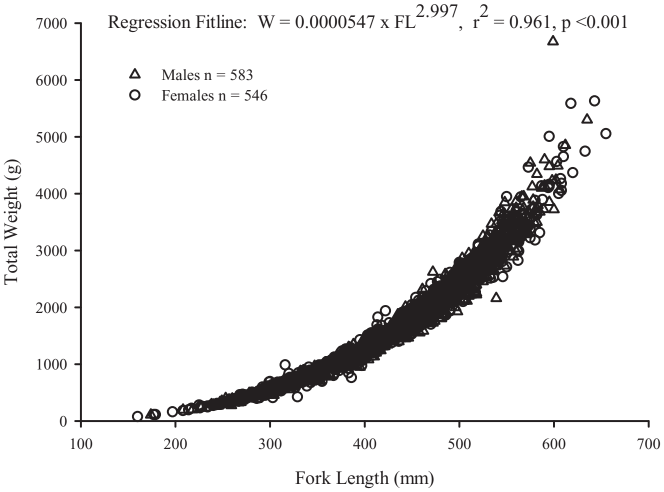

FIGURE 7. Relationship between fork length (FL) and total weight (W) for male and female sheepsheads sampled in South Carolina estuaries from 1990 to 2005.

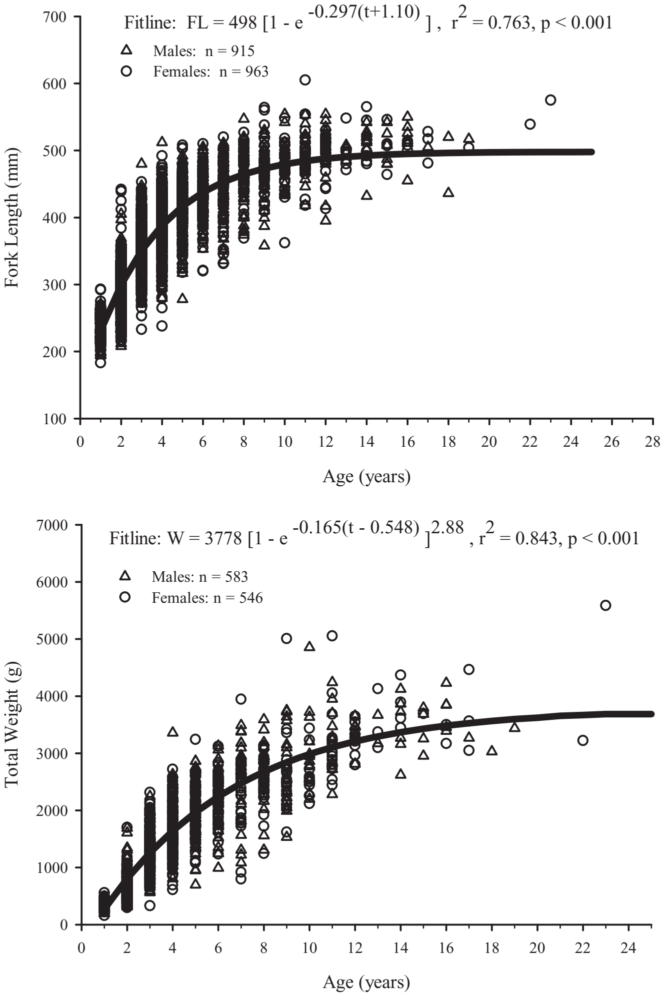

FIGURE 8. Fork length (FL; upper panel) or total weight (W; lower panel) as a function of age (t) for sheepsheads sampled in South Carolina estuaries from 1990 to 2005. Solid lines represent the von Bertalanffy growth curves.

Changes in growth rate coincided with the onset of sexual maturity. Maturity at size and maturity at age differed between males and females ($P = 0.03$), and sex-specific logistic regressions were retained. Fifty percent of males were sexually mature at 250 mm FL and at age 1 (Figure 11). For males, the logistic regressions for size and age at maturity were $Z_{\mathrm{FL}} = -9.532 + 0.038(\mathrm{FL})$ and $Z_{\mathrm{age}} = -1.268 + 0.590(\mathrm{age})$. The logistic regressions for females were $Z_{\mathrm{FL}} = -9.893 + 0.039(\mathrm{FL})$ and $Z_{\mathrm{age}} = -1.585 + 1.521(\mathrm{age})$. Females reached 50% maturity at approximately the same size and age as males (250 mm FL and age 1; Figure 11). Both males and females reached 100% maturity by age 5 and 400 mm FL.

Spawning-capable (fully hydrated) female sheepsheads ($n = 62$) were collected between 20 and 26 April during 2001–2006 and were used for batch fecundity determinations. Water temperatures recorded by the trammel-net survey in Charleston Harbor ranged from 19.6°C to 25.9°C during the April collection periods. The specimens used for fecundity estimates ranged from 282 to 603 mm in FL, from 480 to 5,630 g in weight, and from 2 to 18 years in age (Figure 12). Batch fecundity ranged from 18,400 to 738,500 oocytes/ovary (mean ± SD = 235,700 ± 161,947 oocytes/ovary).

Tournament specimens were collected during April–August, but POFs were only present during April and May. Specimens collected during December–March were not examined histologically because they came from the fish wrack recycling program (i.e., had been frozen). All observed POFs appeared to be older than 24 h according to morphological criteria and the state of atrophy (DeMartini and Fountain 1981; Hunter and Macewicz 1985). The percentage of females with POFs during April and May of each year ranged from 5.0% to 39.1%, which indicated a spawning frequency of 2.5 to 20.0 d. This resulted in a mean (± SD) spawning frequency of 7.6 ± 2.1 d, or approximately once per week. Although the specimens that were examined for batch fecundity came from 12 different age-classes, 71% of the specimens were younger than age 6 and 50% of the specimens were age 3 or 4. Batch fecundity was significantly related to FL ($r^2 = 0.226$, $P < 0.001$), W ($r^2 = 0.229$, $P < 0.001$), and age ($r^2 = 0.145$, $P = 0.003$), although low r^2 values indicated that these variables were poor predictors of fecundity (Figure 12).

DISCUSSION

Aging and Validation

The MIA validated the timing and periodicity of annulus formation in the otoliths of South Carolina sheepsheads. With a spawning season that occurs from late winter into spring (Render and Wilson 1992; Dutka-Gianelli and Murie 2001; present study), the actual ages of sheepsheads were close to the number of annuli, since the opaque zone of each annulus formed close to the end of the spawning season. Marginal increment analysis can provide misleading results for validating

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 27 Dec 2024
Terms of Use: https://bioone.org/terms-of-use

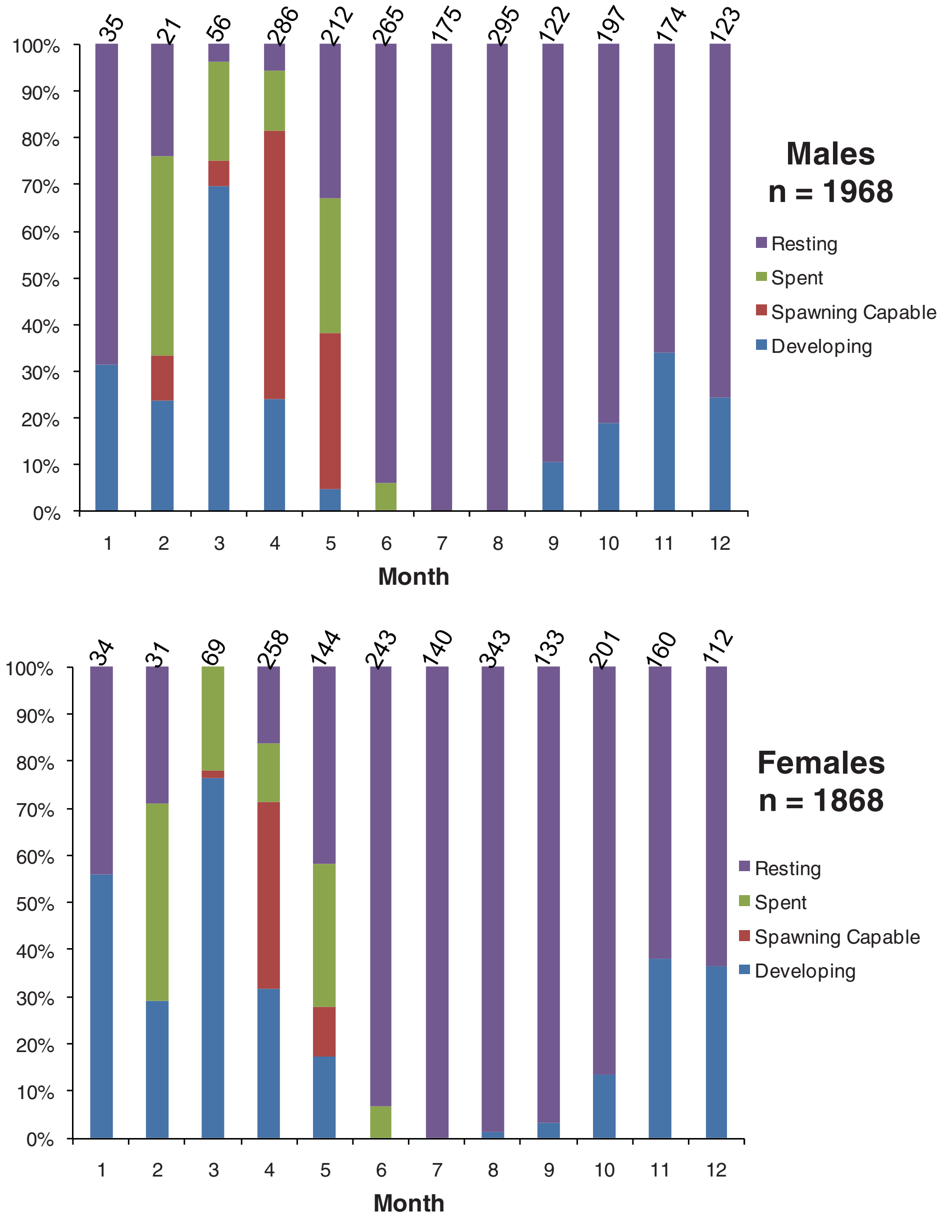

FIGURE 9. Monthly percentages of fish at four sexual maturity stages for sheepshead males (upper panel) and females (lower panel) sampled in South Carolina estuaries from 1990 to 2005. The number above each column indicates the total number of fish examined during each month (month 1 = January; month 12 = December).

an aging method—increment widths and particularly the timing of the first increment deposition are highly variable—when applied to fishes from multiple age-classes over limited periods of the growth cycle (Campana 2001). In addition, for some species the absolute age at the time of the first increment deposition can differ greatly depending on the timing and length of the spawning season (Barger 1985; Barbieri et al. 1993). Even though the first visible marginal increments occurred in May, the narrowest mean marginal increments in this study occurred in July and August, when the annuli were definitively visible and more easily measured. Campana (2001) presented a protocol for validating annular increment seasonality and periodicity by use of MIA: (1) samples should be examined in a randomized fashion; (2) a minimum of two growth cycles should be examined; (3) results should be interpreted objectively; and (4) MIA should be restricted to either a few age-groups or single age-groups. The aging criteria used in the present study adhered to this protocol: 3 years of growth were evaluated, all samples were examined blindly in no particular order, and the deposition of annuli was demonstrated for ages 1–5 individually and in combination.

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 27 Dec 2024
Terms of Use: https://bioone.org/terms-of-use

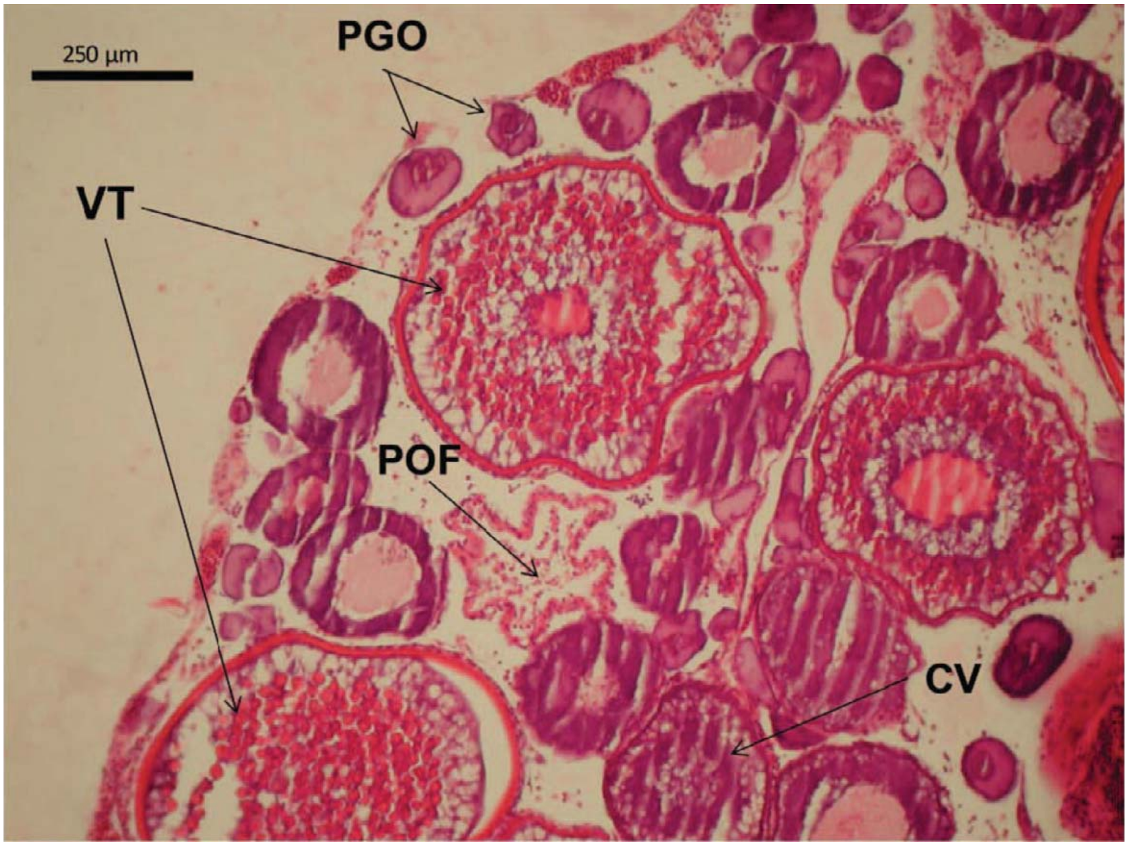

FIGURE 10. Photomicrograph of a developing ovary from a sheepshead collected on 22 April 2004 in South Carolina (PGO = primary growth oocyte; CV = cortical alveolar stage oocyte; VT = vitellogenic stage oocyte; POF = postovulatory follicle).

Annulus deposition in sheepsheads occurred later (May or June) along the Atlantic coast than along the Gulf coast of Louisiana (April or May; Beckman et al. 1991) or Florida (March or April; Dutka-Gianelli and Murie 2001); the later annulus deposition for fish along the Atlantic coast was observed in Georgia (J. L. Fortuna and colleagues, Georgia Department of Natural Resources, unpublished report) and in South Carolina (present study). Sheepsheads range as far north as New York on the U.S. Atlantic coast, and the timing of increment formation observed as far north as Virginia also occurs in May or June (J. Ballenger, Old Dominion University, personal communication). The latitudinal difference in the time of annulus formation along the southeastern U.S. coast is probably related to a temperature effect, resulting in later formation with increasing latitude. The seasonality of annulus deposition in sheepsheads from this study agrees with previous assessments of other fish species in subtropical and temperate latitudes, where the opaque portion of the annular increment forms during the spring and summer months (Barger 1985; Barbieri et al. 1993; Beckman and Wilson 1995).

Growth

Length and weight were not good predictors of age because of the wide range of sizes at a given age, particularly after age 2. For example, in our data, a 2-year-old sheepshead could range from just over 200 to 450 mm in FL and from 300 to 1,500 g in weight, and such variability increased with age. A similar range of sizes at age has been demonstrated for sheepsheads in the Gulf of Mexico (Dutka-Gianelli and Murie 2001).

Statistical comparisons of sheepshead growth among studies conducted in the southeastern United States were hindered by differences in sampling regimes, gear types, and the data matrices used to derive the von Bertalanffy parameters. However, qualitative examination of the available data proved useful for comparing growth differences throughout the southeastern U.S. Atlantic coast and the Gulf of Mexico (Table 1). Sheepsheads from North Carolina and South Carolina appeared to be larger but not necessarily older than sheepsheads in other studies. Larger specimens (weight > 8.5 kg) have been observed in Louisiana, but their ages were not estimated (Beckman et al. 1991). The maximum size of sheepsheads in Georgia (Fortuna and colleagues, unpublished report) was similar to that of fish in South Carolina, whereas sheepsheads from Florida waters had smaller maximum size and age ranges on both the Atlantic and Gulf coasts (Murphy et al. 1997; Dutka-Gianelli and Murie 2001). Comparisons of estimated L_∞ from the von Bertalanffy growth curves showed that although values for South Carolina,

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 27 Dec 2024
Terms of Use: https://bioone.org/terms-of-use

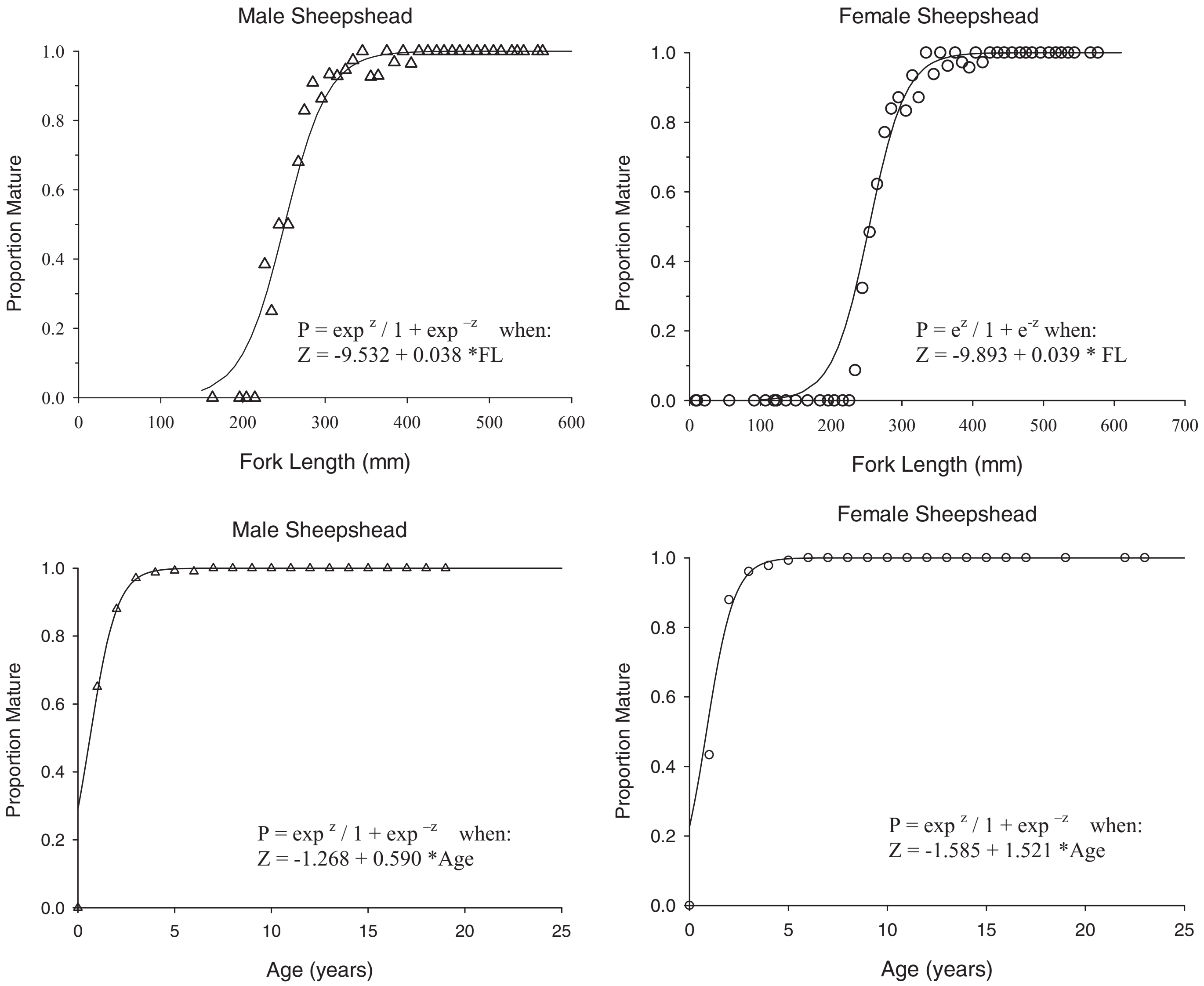

FIGURE 11. Proportion (*P*) of males and females that were mature at each fork length (FL) and age for sheepsheads sampled in South Carolina estuaries from 1990 to 2005 ($Z =$ logistic regression *Z*-function value). Solid line represents the equation fitline; symbols represent the raw data.

northwest Florida (Dutka-Gianelli and Murie 2001), and Georgia (Fortuna and colleagues, unpublished report) were roughly equal, the L_∞ values for the Florida Atlantic coast (Murphy et al. 1997) and Louisiana (Beckman et al. 1991) were noticeably smaller.

The range of *k*-values was similar for sheepsheads in northwest Florida (Dutka-Gianelli and Murie 2001) and Georgia (Fortuna and colleagues, unpublished report) but was slightly higher for fish in South Carolina. However, *k* was noticeably higher for sheepsheads along the Florida Atlantic coast (Murphy et al. 1997) and in Louisiana (Beckman et al. 1991; Table 1). Asymptotic length is inversely related to *k*, and a decrease in *k* results in an increase in L_∞ (Campana 2001). Thus, although the data matrices from the different studies could only be compared qualitatively, they all exhibited the expected behavioral relationships between the von Bertalanffy parameters for a normalized age distribution.

The wide range of lengths and estimated growth parameters for sheepsheads appeared to depend on the area and the sampling methodology. This could be the result of varying fishing pressure (recreational and commercial), environmental or habitat conditions, and perhaps population genetic characteristics. It has been shown that sheepsheads move offshore to spawn (Jennings 1985), but the extent of this movement and whether any segment of the population remains offshore are not known. Recent genetic evidence indicates that the two apparent sheepshead subspecies in the Gulf of Mexico are actually a single population with genetic variation attributed to geographic

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 27 Dec 2024
Terms of Use: https://bioone.org/terms-of-use

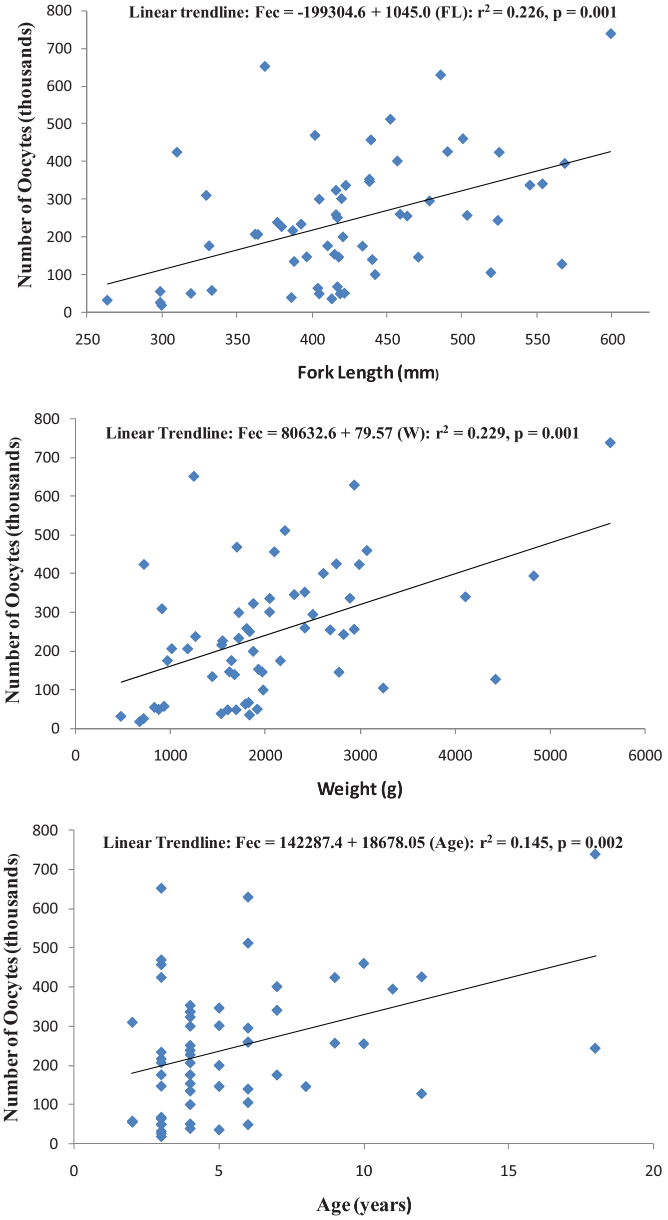

FIGURE 12. Batch fecundity (Fec; oocytes/batch) as a function of fork length (FL), weight (*W*), and age for female sheepsheads sampled in South Carolina estuaries from 2001 to 2006.

differences (Anderson et al. 2008). Although there might be limited genetic differences between subpopulations in different regions, the differences in sheepshead growth could suggest an underlying population structure with limited latitudinal movement for this species. Additionally, movement between inshore and offshore habitats precludes the separation of any component of the sheepshead population into discrete population subunits. Therefore, sheepshead growth in South Carolina could only be considered at the general population level, for which the major factors influencing growth dynamics are fishing pressure and environmental conditions.

There may have been gear bias in the size distribution of sheepsheads collected from fishing tournaments and other recreational fishing sources, as tournament anglers target larger fish and are less likely to report small fish. In this study, the length distribution of the trammel-net samples differed from that of fish sampled by the fishery-dependent gear; the difference was primarily associated with the greater abundance of smaller size-classes (<200 mm FL) in the trammel-net samples. However, the maximum length of sheepsheads (595 mm FL) caught in the trammel nets corresponded closely with that of angler-caught fish (603 mm FL). Therefore, although there may have been some bias toward larger fish in the tournament data, the similarity in size ranges between the fishery-independent (trammel net) and fishery-dependent (hook and line) gear types indicated that the estimated size distribution of sheepsheads in South Carolina was reasonable.

Offshore specimens collected in this study came from the fish wrack recycling program, and 64% of these fish were captured in March and April (the last months of the spawning season). Capture locations for the fish wrack specimens were generally within 16.093 km (10 mi) of the freezer location at which the specimens were dropped off, and sheepshead anglers do not typically go very far offshore to fish. Thus, even the specimens caught outside of the estuaries were generally captured at nearshore reef sites. Summary data from the MRFSS (NMFS 2006) indicated that the total catches during this time period (March and April) were higher in federal waters (>5.556 km [3 nautical miles] from the shore) than in nearshore state waters (<5.556 km from shore) and inshore waters, despite nearshore effort being two to three times greater than effort in federal waters. During the remainder of the year (from May to February), both catch and effort were higher in nearshore waters compared with federal waters. Similar trends in catch by area fished have been demonstrated for the spawning season in Georgia (Music and Pafford 1984; Fortuna and colleagues, unpublished report), and the bulk of the catch during that time originated from federal waters. In the Gulf of Mexico, the bulk of recreational landings during the spawning season are obtained in state waters instead of federal waters because the state jurisdiction extends to 16.668 km (9 nautical miles) in this region. The higher offshore catches along the Atlantic coast during the spawning season probably arise due to the targeting of spawning aggregations at that time.

Fishing pressure on sheepsheads in South Carolina waters during the spawning season appeared to be high, but the lack of sexually dimorphic growth and the relatively consistent 1:1 sex ratio suggest that males and females are affected equally. Another fishery-related explanation that could influence growth parameters between the different states could be the differences in fishery regulations. In South Carolina, sheepsheads are managed federally: there is no length restriction, and the bag limit is 20 fish·person^{-1}·d^{-1}. On the southeastern U.S. Atlantic coast, both Florida and Georgia impose additional state regulations, including minimum TLs of 25.4 and 30.5 cm (10 and 12 in),

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 27 Dec 2024
Terms of Use: https://bioone.org/terms-of-use

TABLE 1. Parameters of the von Bertalanffy growth equation (L_∞ = asymptotic length; k = growth coefficient), maximum fork length (FL), and maximum age of sheepsheads as observed during the present study and during previous studies in the southeastern USA.

Data source	Location	Sex	L_∞	k	Maximum FL (mm)	Maximum age (years)
Present study	South Carolina	Male	499	0.299	567	19
		Female	498	0.296	603	23
		Pooled	498	0.297	603	23
Schwartz 1990	North Carolina	Pooled			673[a]	8[b]
Fortuna and colleagues, unpublished	Georgia	Male	495	0.233	580	18
		Female	502	0.212	580	18
		Pooled	498	0.218	580	18
Dutka-Gianelli and Murie 2001	Northwest Florida	Male	509	0.23	522	12
		Female	476	0.28	505	14
		Pooled	490	0.260	522	14
Murphy et al. 1997	Florida (Gulf coast)	Pooled	449	0.200		11–14
	Florida (Atlantic coast)	Pooled	405	0.330		11–14
Beckman et al. 1991	Louisiana	Male	419	0.370	505	20
		Female	446	0.420	563	20

[a] Data were originally reported as total length and were converted to FL by using the total length–FL relationship from the present study.

[b] Ages were determined by use of scales.

respectively, as do most of the Gulf coast states. Such regulatory differences could affect estimates of growth parameters from states that use fishery-dependent data by gradually reducing the number of faster-growing or larger fish in the general population, thus reducing mean size at age and accounting for the lower values of k in these areas.

Maturity and Fecundity

Approximately 50% of male sheepsheads in South Carolina were sexually mature by age 1, and 80% were mature by age 2. Fewer females showed signs of reproductive development by age 1 (~40%), but the majority (>90%) of fish of both sexes were mature by age 3. These estimates of age at first maturity were 1 year earlier than those reported for sheepsheads from Louisiana (Render and Wilson 1992). The earlier age at first maturity in the present study was probably due to the sampling of younger age-classes that were not examined by Render and Wilson (1992).

Reproductive development in male and female sheepsheads in South Carolina was apparent from December into early May based on both histological examinations and macroscopic staging; however, spawning-capable (hydrated) females were only observed during February through early May. This agrees with observations of sheepsheads in the Gulf of Mexico, where spawning occurred from late winter into early spring (Jennings 1985; Beckman et al. 1991; Render and Wilson 1992). Juvenile sheepsheads (10–30 mm FL) in South Carolina have been observed to recruit to estuarine habitats during April–June (SCNDR, unpublished data). Given a 30–40-d time period before settlement (Jennings 1985), these newly recruited juveniles were probably spawned between February and April. Spent testes and ovaries undergoing atresia were observed in February–June and POFs were present in April and early May, thus providing evidence that spawning ceased by mid-May. Collectively, these results indicate a spawning season of February–early May for sheepsheads in South Carolina. The presence of spent specimens in February and March indicates that although the spawning season may run from February through May, individual sheepsheads do not necessarily spawn throughout the entire season. In addition, there was no evidence of sheepshead spawning in estuarine waters of South Carolina, contrary to the estuarine spawning that was documented in Louisiana (Render and Wilson 1992).

The range of batch fecundities from this study was broad (18,400–738,500 oocytes/batch); despite the positive correlation of fecundity to FL, W, and age, fish size and age were poor predictors of batch fecundity. This was particularly evident for age due to the wide range in fecundity at all ages. Fecundity samples from this study were limited in scope due to the limited time period in which the specimens were collected (i.e., at the end of spawning season). Batch fecundity values were higher for sheepsheads from South Carolina (mean fecundity = 235,700 oocytes/batch) than for sheepsheads from the Gulf of Mexico (mean fecundity = 47,000 oocytes/batch; Render and Wilson 1992). The technique used in both studies was similar (based on Hunter and Macewicz 1985), so the difference in results may be due to differences in the size range and number of fish sampled (n = 62 in the present study; n = 20 in the Render and Wilson [1992] study). Render and Wilson (1992) did not analyze batch fecundity by fish size, but they did partition fish between inshore and offshore groups and found higher batch fecundity values (mean fecundity = 87,000

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 27 Dec 2024
Terms of Use: https://bioone.org/terms-of-use

oocytes/batch; range = 14,000–250,000 oocytes/batch) for the offshore group, which contained predominantly older and larger individuals than the inshore group. However, fecundity levels in both groups were still less than those measured in the present study.

Spawning frequency determinations based on POFs were also common to both this study and the study by Render and Wilson (1992). The estimated spawning frequency determined in the present study (2.5–20.0 d) was very similar to the range reported by Render and Wilson (1992: 1–20 d). However, Render and Wilson (1992) expressed a high level of uncertainty in their spawning frequency estimates because of the small sample size, despite sampling throughout the spawning season. Since maturity assessments in our study indicated that the bulk of spawning activity occurred from February to April, the fish used in the fecundity analysis represented the very end of the spawning season. With an approximately weekly spawning frequency and a spawning season of 14 weeks (February–early May), total annual fecundity could range from 250,000 to 10,339,000 oocytes$\cdot$female$^{-1}\cdot$year^{-1} depending on size and age. Better estimates of annual fecundity could be obtained by sampling additional females from earlier in the spawning season, which would allow an assessment of whether batch fecundity or spawning frequency changes during the spawning season. Although this would give a better overall view of reproductive output for sheepsheads, the relative levels of batch fecundity based on fish size and age and the estimates of spawning frequency reported here are still useful given the limited availability of sheepshead fecundity data in the literature (Render and Wilson 1992).

There is much additional potential for sheepshead research in South Carolina. Our study indicated the existence of broad size and age ranges for sheepsheads in South Carolina. Recreational harvest data from the MRFSS (NMFS 2006) suggest that the majority of fishing pressure for sheepsheads occurs in state waters despite the species being managed at the federal level as part of the offshore snapper–grouper complex. Without more extensive fishery-independent data from state waters, the full impact of recreational fishing pressure on sheepsheads will be difficult to discern. Additionally, more extensive life history studies on reproductive development and fecundity are necessary to permit the assessment of fishery impacts on sheepshead spawning aggregations off the coast of South Carolina. Given the differences in sheepshead growth among the various regions of the southeastern United States and given the level of fishing pressure that occurs in state waters, a more localized approach to the management of this species may be warranted to maintain adequate spawning biomass and to ensure recruitment for future years.

ACKNOWLEDGMENTS

We acknowledge past and present members of the Inshore Fisheries group, SCDNR Marine Resources Research Institute, for facilitating field collections, officiating at tournaments, and processing samples in the laboratory. In addition, much of the data could not have been collected without the participation of tournament anglers and recreational fishermen from the fish wrack recycling program (administered by J. Archambault), which was funded through the South Carolina State Recreational Fisheries Advisory Committee. We particularly thank J. Boynton for the map figure and E. Levesque, R. Freeman, G. Perez, and H. Von Kolnitz for otolith processing and age determination. We are grateful to S. Arnott, M. Denson, and J. Ballenger for providing careful review and suggestions for this manuscript. This is Contribution Number 688 of the Marine Resources Research Institute (South Carolina Department of Natural Resources, Charleston).

REFERENCES

Anderson, J. D., W. J. Karel, K. A. Anderson, and P. A. Roper-Foo. 2008. Genetic assessment of sheepshead stock structure in the northern Gulf of Mexico: morphological divergence in the face of gene flow. North American Journal of Fisheries Management 28:592–606.

Barbieri, L. R., M. E. Chittenden, and C. M. Jones. 1993. Age, growth, and mortality of Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay region, with a discussion of apparent changes in population dynamics. U.S. National Marine Fisheries Service Fishery Bulletin 92:1–12.

Barger, L. 1985. Age and growth of Atlantic croakers in the northern Gulf of Mexico, based on otolith sections. Transactions of the American Fisheries Society 114:847–850.

Beckman, D. W., A. L. Stanley, J. H. Render, and C. A. Wilson. 1991. Age and growth-rate estimation of sheepshead, *Archosargus probatocephalus* in Louisiana waters using otoliths. U.S. National Marine Fisheries Service Fishery Bulletin 89:1–8.

Beckman, D. W., and C. A. Wilson. 1995. Seasonal timing of opaque zone formation in fish otoliths. Pages 27–43 *in* D. H. Secor, J. M. Dean, and S. E. Campana, editors. Recent developments in fish otolith research. University of South Carolina Press, Columbia.

Beverton, R. J., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Chapman and Hall, London.

Boehlert, G. W. 1985. Using objective criteria and multiple regression models for age determination in fishes. U.S. National Marine Fisheries Service Fishery Bulletin 83:103–117.

Brown-Peterson, N. J., D. M. Wyanski, F. Saborido-Rey, B. J. Macewicz, and S. K. Lowerre-Barbieri. 2011. A standardized terminology for describing reproductive development in fishes. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 3:52–70.

Caldwell, D. K. 1965. Systematics and variation in the sparid fish *Archosargus probatocephalus*. Bulletin of the Southern California Academy of Sciences 4:89–100.

Campana, S. E. 2001. Accuracy, precision, and quality control in age determination, including a review of the use and abuse of age validation methods. Journal of Fish Biology 59:197–242.

Campana, S. E., S. E. Annand, and J. I. McMillan. 1995. Graphical and statistical methods for determining the consistency of age determinations. Transactions of the American Fisheries Society 124:131–138.

Chang, W. Y. B. 1982. A statistical method for evaluating the reproducibility of age determinations. Canadian Journal of Fisheries and Aquatic Sciences 39:1208–1210.

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. U.S. National Marine Fisheries Service Fishery Bulletin 79:547–560.

Dutka-Gianelli, J., and D. J. Murie. 2001. Age and growth of sheepshead, *Archosargus probatocephalus* (Pisces: Sparidae), from the northwest coast of Florida. Bulletin of Marine Science 68:69–83.

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 27 Dec 2024
Terms of Use: https://bioone.org/terms-of-use

Fitzhugh, G. R., and W. F. Hettler. 1995. Temperature influence on postovulatory follicle degeneration in Atlantic menhaden, *Brevoortia tyrannus*. U.S. National Marine Fisheries Service Fishery Bulletin 93:568–572.

Hoenig, J. M., M. J. Morgan, and C. A. Brown. 1995. Analyzing differences between two age determination methods by tests of symmetry. Canadian Journal of Fisheries and Aquatic Sciences 52:364–368.

Humason, G. L. 1967. Animal tissue techniques. Freeman, San Francisco.

Hunter, J. R., and B. J. Macewicz. 1985. Measurement of spawning frequency in multiple spawning fishes. Pages 79–94 *in* R. Lasker, editor. An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. NOAA Technical Report NMFS 36.

Jennings, C. A. 1985. Species profiles, life histories and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico) – sheepshead. U.S. Fish and Wildlife Service Biological Report 82(11.29). U.S. Army Corps of Engineers, TR EL-82-4, Vicksburg, Mississippi.

Johnson, D. G. 1978. Development of fishes in the mid-Atlantic Bight: an atlas of egg, larval, and juvenile stages, volume 4 Carangidae through Ephippidae. U.S. Fish and Wildlife Service FWS/OBS-78/12.

Lehnert, R. L., and D. M. Allen. 2002. Nekton use of sub-tidal oyster shell habitat in a southeastern U.S. estuary. Estuaries 25:1015–1024.

Murphy, M. D., B. Mahmoudi, and R. G. Muller. 1997. A stock assessment of sheepshead. Report from the Florida Marine Research Institute, St. Petersburg, to the Florida Marine Fisheries Commission, IHR1997-004 Tallahassee.

Music, J. L., and J. M. Pafford. 1984. Population dynamics and life history aspects of major marine sportfishes in Georgia's coastal waters. Georgia Department of Natural Resources, Federal Aid in Sport Fish Restoration Act, Project F-31, Contribution Series 38, Final Report, Brunswick.

NMFS (National Marine Fisheries Service). 2006. Marine Recreational Fisheries Statistics Survey. NMFS Statistics and Economics Division. Available: http://www.st.nmfs.noaa.gov/st1/recreational/index.html. (August 7, 2007).

Odum, W. E., and E. J. Heald. 1972. Trophic analysis of an estuarine mangrove community. Bulletin of Marine Science 22:671–738.

Parsons, G. R., and K. M. Peters. 1987. Age determination in larval and juvenile sheepshead, *Archosargus probatocephalus.* U.S. National Marine Fisheries Service Fishery Bulletin 87:985–988.

Render, J. H., and C. A. Wilson. 1992. Reproductive biology of sheepshead in the northern Gulf of Mexico. Transactions of the American Fisheries Society 121:757–764.

Roumillat, W. A., and M. C. Brouwer. 2004. Reproductive dynamics of female spotted seatrout (*Cynoscion nebulosus*) in South Carolina. U.S. National Marine Fisheries Service Fishery Bulletin 102:473–487.

Schwartz, F. J. 1990. Length-weight, age and growth, and landings observations for sheepshead, *Archosargus probatocephalus* from North Carolina. U.S. National Marine Fisheries Service Fishery Bulletin 88:829–832.

Secor, D. H., J. M. Dean, and S. E. Campana. 1995. Recent developments in fish otolith research. University of South Carolina Press, Columbia.

Springer, V. G., and K. D. Woodburn. 1960. An ecological study of the fishes of the Tampa Bay area. Florida Board of Conservation and Marine Laboratory Professional Papers Series 1.

Tucker, J. W., and S. R. Alshuth. 1997. Development of laboratory reared sheepshead, *Archosargus probatocephalus* (Pisces: Sparidae). U.S. National Marine Fisheries Service Fishery Bulletin 95:394–401.

Wenner, C. A., and J. Archambault. 2006. Sheepshead: natural history and fishing techniques in South Carolina. South Carolina Department of Natural Resources, Marine Resources Research Institute, Educational Report 23, Charleston.

Wenner, C. A., W. A. Roumillat, and C. W. Waltz. 1986. Contributions to the life history of black seabass, *Centropristis striata*, off the southeastern United States. U.S. National Marine Fisheries Service Fishery Bulletin 84:723–741.

Zar, J. H. 1984. Biostatistical analysis, 2nd edition. Prentice-Hall, Englewood Cliffs, New Jersey.

Downloaded From: https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 27 Dec 2024
Terms of Use: https://bioone.org/terms-of-use