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ARTICLE

Age, Growth, and Reproduction in Two Coastal Populations of Longnose Gars

Meredith Smylie*[1]
Grice Marine Laboratory, College of Charleston, 205 Fort Johnson Road, Charleston, South Carolina 29412, USA

Virginia Shervette
Department of Biology and Geology, University of South Carolina–Aiken, 471 University Parkway, Aiken, South Carolina 29801, USA

Chris McDonough
South Carolina Department of Natural Resources, Marine Resources Division, 217 Fort Johnson Road, Charleston, South Carolina 29422, USA

Abstract

Measurements of age, growth, and reproduction are excellent tools for determining the ecological role and impact of a species within an ecosystem. Longnose Gar *Lepisosteus osseus* is a large, ubiquitous top predator in fresh and saline waters of the eastern United States. Even though the species is common, their basic biology has been largely uncharacterized in brackish and marine waters. Specimens were collected from two estuaries: Winyah Bay and Charleston Harbor, South Carolina, from May 2012 through July 2013 to examine age, growth, and reproduction in tidally influenced systems. This species is fairly long-lived, with maximum ages of 17 and 25 years for males and females, respectively. The von Bertalanffy growth model yielded significantly higher growth rates for males than for females. Reproductive histology and the gonadosomatic index indicated that Longnose Gars exhibit determinate fecundity and spawn in late spring following a long development period during fall and winter. These life history parameters provide valuable insight into the basic biology of Longnose Gars and into how they function in estuarine environments. Further research on the precise timing and location of spawning movement, as well as daily movement patterns of this species, would provide a more comprehensive knowledge of Longnose Gar reproductive biology.

The Longnose Gar *Lepisosteus osseus* ranges across the eastern half of North America as far north as the St. Lawrence River in Quebec, west throughout the lower Missouri River basin and tributaries of the Mississippi River, south to the coast of Texas, and east to the Atlantic coast from northern Florida up through parts of New England (Haase 1969; Wiley 1976; Lee et al. 1980; Boschung and Mayden 2004). Longnose Gars occur mostly in freshwater rivers, oxbow lakes, sloughs, backwaters, swamps, reservoirs, and high-gradient areas of tributaries (Robison and Buchanan 1988; Boschung and Mayden 2004) but are capable of tolerating moderately saline waters (Hildebrand and Schroeder 1928; Goodyear 1967; McGrath 2010; Henzler 2011). The elongate body form of gars (family Lepisosteidae) promotes their ambush feeding strategy, allowing a fish to float effortlessly, mimicking a submerged branch to unsuspecting prey that venture near

*Corresponding author: meredithsmylie@gmail.com
[1]Present address: Greeley Memorial Laboratory, Yale University, 370 Prospect Street, New Haven, Connecticut 06511, USA.
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enough so the gar can rapidly burst towards the food and catch it with its large villiform teeth. Gar species possess a physostomous gas bladder, which allows them to inhabit low-oxygen waters that may exclude other top predators (Potter 1926; Snedden et al. 1999). Longnose Gar adults can travel large distances to spawn in upstream waters in late spring and early summer, though their precise movement patterns remain largely unknown throughout much of their range (Netsch and Witt 1962; McGrath 2010).

Longnose Gars are often referred to as an apex predator, opportunistically feeding on abundant prey, including a variety of fishes, invertebrates, and even terrestrial vertebrates (Robertson et al. 2008; Henzler 2011). This feeding strategy, in addition to their prehistoric look and high abundance throughout much of their range, may be partially responsible for their reputation as a nuisance species, sometimes perceived as detrimental to game fish (Johnson and Noltie 1996).

Given the ubiquity of Longnose Gars in the freshwater and estuarine systems of the eastern United States and their importance as an upper trophic level predator, there is a need for basic biological knowledge for this species. To date, no peer-reviewed published study provides a comprehensive description of the age, growth, and reproduction of Longnose Gars. There are a few studies examining population age structure in Longnose Gars, which all utilized branchialstegal rays for age estimation (Netsch and Witt 1962; Klaassen and Morgan 1974; Johnson and Noltie 1996; Sutton et al. 2009; Kelley 2012), even though it has been demonstrated that otoliths provide better estimates of age in fish than do other structures (Buckmeier et al. 2002; Sylvester and Berry 2006; Ma et al. 2011; Buckmeier et al. 2012). A few studies have described some aspects of reproduction in Longnose Gars (gonadosomatic index and fecundity), but none utilized histological techniques to describe the reproductive cycle (Netsch and Witt 1962; Johnson and Noltie 1996; Zeug and Winemiller 2007). Therefore, the purpose of this study was to investigate these key life history attributes for two populations of this species from coastal South Carolina. Specifically, we wanted to do the following: (1) document population age structure and growth rates using sagittal otoliths, (2) describe reproductive phases of males and females using histological techniques, (3) quantify sex-specific monthly changes in the gonadosomatic index (GSI), and (4) quantify female potential annual fecundity.

METHODS

Study sites.—Our study occurred within two South Carolina estuaries, the Winyah Bay–Pee Dee–Black River system (referred to as Winyah Bay) and the Charleston Harbor–Wando–Cooper–Ashley River system (referred to as Charleston Harbor). Winyah Bay (Figure 1) is a piedmont estuary system (Dame et al. 2000) that is the confluence of coastal plain rivers (Sampit, Black, and Waccamaw) and piedmont rivers (Little Pee Dee and Great Pee Dee). The coastal plain rivers are characterized by low flow, small watersheds located completely within the coastal plain, extensive wetlands, and a large brackish area. These rivers are commonly called "blackwater" due to the color resulting from excessive tannins and other decomposing organic material (Dame et al. 2000) and are characterized by low pH and low flushing rates where they open into Winyah Bay (SCDHEC 2013a). The piedmont rivers, by contrast, have large watersheds, considerable freshwater input, and relatively small associated wetlands. These rivers converge near Georgetown, South Carolina, resulting in an extensive marsh and estuary complex (Dame et al. 2000). Winyah Bay is fed from a 45,163-km^2 watershed impacted by agricultural and industrial production (Guentzel and Tsukamoto 2001). This water system is fairly shallow with an average depth of 3 m, a tidal range of approximately 0.8 m, and salinities up to 34‰ (Dame et al. 2000). In the lower portions of the bay, pH increases and dissolved oxygen declines relative to that in the upper portion (SCDHEC 2013a).

The Charleston Harbor estuary (Figure 1) is composed of three converging coastal plain rivers, the Ashley, Cooper, and Wando, with a small drainage of about 900 km^2 (Knott and Martore 1991) and little freshwater input, making the salinity relatively stable (Dame et al. 2000). The Ashley River originates in Berkeley County, South Carolina, and is characterized by steadily increasing pH and dissolved oxygen over time and decreasing nitrogen in upriver areas (SCDHEC 2013c). Elevation sharply increases along this river potentially due to tectonic upwarping, which results in dry, higher elevated land on the western side of the river and extensive salt marsh to the east. Tectonics have a smaller impact in the more upriver portions, where extensive swamp, characterized by branching and reconverging streams, is dominant (Marple and Talwani 1993). This swampy region also contains a number of small ponds, including Schultz Lake, which was sampled during the present study (Figure 1). The Cooper River originates in Lake Moultrie and has controlled flow rates with high turbidity and average but increasing pH and dissolved oxygen from the headwaters to the mouth (SCDHEC 2013d). The Wando River flows through Berkeley and Charleston counties before intersecting the Cooper River (SCDHEC 2013b). These three rivers converge around Charleston, South Carolina, forming the Charleston Harbor estuary, which is characterized by an average depth of 4.9 m and a tidal range of 1.4 m and is generally more saline than Winyah Bay (Dame et al. 2000).

Sampling methods.—The Longnose Gars for this study were collected from May 2012 through July 2013 by the South Carolina Department of Natural Resources (SCDNR) mainly as part of two fishery-independent statewide coastal monitoring programs: the trammel net survey and the electrofishing survey. The trammel net survey uses a stratified-random-sampling protocol in seven estuaries (two of which are our Charleston Harbor and Winyah Bay estuarine systems). Each

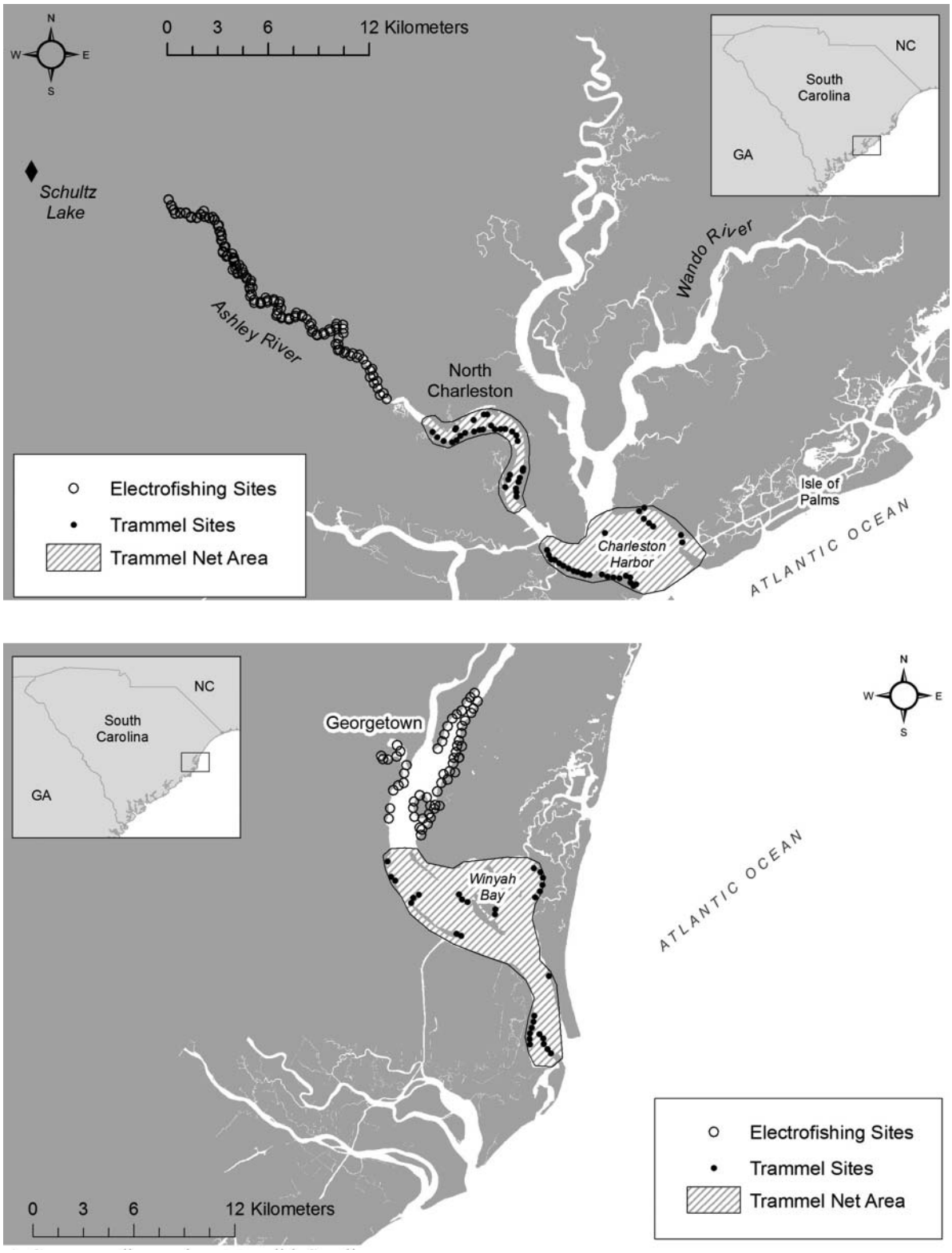

FIGURE 1. Map of the sampling sites within the Charleston Harbor and Winyah Bay estuaries in South Carolina.

individual estuary is a separate stratum and sampling sites within estuaries are chosen at random on a monthly basis. This means that each month 10–12 sites per estuary are normally chosen for sampling; however, this number is not always achieved due to weather, tide, or time limitations. The electrofishing survey also uses a monthly stratified-random-sampling design and was initiated to complement the trammel net survey by sampling the low-salinity brackish and tidal freshwater portions of estuaries, where the trammel nets are not effective.

The trammel net survey consists of collecting fish using a three-layered net system that is 182 m × 2 m and fitted with polyfoam float line and lead core bottom line. The netting is comprised of an inner panel of monofilament mesh (64-mm stretched mesh with a height of 60 diagonal meshes) between a pair of outer panels of monofilament mesh (356-mm stretched mesh with a height of 8 diagonal meshes). The trammel net is deployed along the shoreline 10–20 m from an intertidal marsh flat in water less than 2 m deep during an ebbing tide and the ends are anchored on the shore or in shallow marsh. Once the net is set, the boat makes two passes along the length of the net at idle speed, during which time the water surface is disturbed with large wooden poles and the hull of the boat is banged with small wooden clubs to promote fish entrapment. The net is then immediately retrieved and fish are removed from the mesh.

The electrofishing survey consists of collecting fish with an electrofishing boat (Smith-Root) operating at approximately 3,000-W pulsed direct current. Stunned fish are collected from the water using dip nets (4.5-mm square mesh) over a 15-min period while the boat moves with the current at drift or idle speed along the riverbank.

Live total length (TL) measurements were taken for each Longnose Gar upon capture (referred to as the total gar sample). A maximum of 10 Longnose Gars from each 100-mm TL size-class (1–1,100+ mm) were retained for life history analysis (referred to as the life history subsample) from each estuarine system per month, with approximately half coming from each sampling method. During March–April 2013, additional Longnose Gar samples were obtained as bycatch from another monitoring program that utilized electrofishing to sample large Striped Bass *Morone saxatilis* in the upper reaches of the Ashley River (Charleston Harbor).

Samples kept for full analysis had the following measurements taken upon return to the laboratory: TL and standard length to the nearest millimeter, total weight (g), and gonad weight (0.001 g). Sagittal otoliths were removed, rinsed, and stored dry for later age determination. The gonads of sacrificed fish were preserved in 10% seawater-buffered formalin immediately after fish processing.

Age and growth.—Sagittal otoliths were embedded in epoxy resin and sectioned (0.4–0.6 mm thick) longitudinally through the primordium, which is located near the distal anterior edge (Figure 2), using a low-speed saw with a high-concentration diamond-edged blade. Otolith sections were mounted on glass slides and examined with a dissecting microscope (30×) using transmitted light. Increments (one translucent and one opaque zone) were counted by two independent readers with no reference to fish size or date of capture. Age estimates (based on increment counts) were compared between readers to determine the percentage of age estimates that agreed exactly, agreed within 1 year, and agreed within 2 years. Additionally, we computed the average percent error between the ages assigned by the readers using the following equation (Beamish and Fournier 1981):

FIGURE 2. Sagittal otolith of a Longnose Gar. The black line indicates the plane of sectioning for age analysis.

$$\frac{1}{N}\sum_{j=1}^{N}\left[\frac{1}{R}\sum_{i=1}^{R}\frac{|X_{ij}-X_j|}{X_j}\right], \quad (1)$$

where N is the number of aged samples, R is the number of times a fish was aged, X_{ij} is the ith age determination of the jth fish, and X_j is the average age calculated for the jth fish.

Increment counts were considered age estimates because a true age validation has not been conducted for this species. Otolith sections for which reader disagreement occurred were reevaluated simultaneously by both readers, and a consensus count was recorded as the final age estimate in whole years. Otolith section margins were evaluated as either containing the final opaque zone along the edge or containing the final translucent zone along the edge. The timing of annulus formation was estimated by examining the monthly percentage of otoliths with opaque zones at the otolith edge for fish age 2–12. Fractional age estimates for Longnose Gars were calculated based on the date of capture and a presumed birth date of May 1, which took into account when opaque bands were laid down (March–May) and when spawning season peaked (April–May; see Results).

To evaluate growth, the observed individual lengths at age were fitted to the von Bertalanffy growth equation as follows:

$$L_t = L_\infty (1 - e^{-k(t - t_0)}), \tag{2}$$

where L_t is the length at age t, L_∞ is the asymptotic length, k is the growth rate, and t_0 is a theoretical age at which the TL is presumed equal to 0 (von Bertalanffy 1938). This model was applied to males and females separately.

Reproduction.—For histological confirmation of sex and determination of maturity, a sample of gonad tissue was removed from sacrificed fish that had not been frozen. Tissues were processed using a standard methodology for histological paraffin embedding and hematoxylin and eosin Y staining (Humason 1967). Maturity and reproductive phases for the histological samples were assessed according to a modified version of classifications in Brown-Peterson et al. (2011) (Figures 3, 4). Specifically, female "developing" was subdivided into early and middle developing based on the classifications of Smith (2008) for Spotted Gar *Lepisosteus oculatus* (Table 1). Phases were determined independently by two readers, samples for which reader disagreement occurred were reevaluated simultaneously by the readers, and a consensus phase was recorded.

Potential annual fecundity was estimated gravimetrically from each mature female captured from November 2012 through July 2013 based on the classifications of Hunter et al. (1992). Formalin-preserved ovarian tissue was divided into six sections: proximal, medial, and distal for each of the two ovaries (Figure 5). Three of these sections were randomly selected as subsamples from each individual. Subsamples weighed 1–2% of the total gonad weight and were removed, rinsed with water, and stored in vials of 70% alcohol until the well-developed oocytes were counted. The GSI was calculated for females using the following equation:

$$\text{GSI} = \frac{\text{Gonad Weight}}{\text{Total Weight}} \times 100. \tag{3}$$

Statistical analysis.—To determine if the fish from the life history subsample represented a similar size distribution to the fish from the total gar sample, we used a Kolmogorov–Smirnov two-sample test (Sokal and Rohlf 1981). To describe the relationship between log-transformed fish TL and weight, we used linear regression analysis. This relationship was also compared between the sexes using analysis of covariance (ANCOVA). To test for differences in size-frequency and age-frequency distributions between sexes, river systems, and sampling methods, we used separate Kolmogorov–Smirnov two-sample tests. The von Bertalanffy growth model was initially applied to males and females together to estimate L_∞, k, and t_0 using a two-stage least-squares regression including a sex term. Because sex was significant, the growth model was then run separately for both sexes. Growth analyses were done using SYSTAT.

A chi-square test was used to determine if significant differences existed in the sex ratio for each estuarine system and between freshwater (≤5‰) and brackish or saltwater collections (>5‰). The proportion of mature Longnose Gars in each size-class (100-mm-TL bins) and age-class was examined by using a binary logistic regression: $Z = a + b \times$ (TL or age), where Z is the logistic regression Z-function value, a is the intercept, and b is the slope. Logistic regressions were run for both sexes. The maturity probability was determined using the following equation:

$$P_{\text{maturity}} = \frac{e^z}{1 + e^{-z}}, \tag{4}$$

where P_{maturity} is the probability of maturity at a given size or age and Z is the estimate from the logistic regression. Nested analysis of variance (ANOVA) was used to test for bias in fecundity estimation associated with the location of the subsample within the ovary (replicate). Nested ANOVA was selected because it avoids pseudoreplication by treating subsamples as part of a replicate instead of as independent replicates.

Due to the highly linear nature of the data, we used separate linear regressions to examine the relationships between female weight and fecundity and between female size (standard length) and fecundity. To determine if the number of oocytes per gram of ovary (relative fecundity) differed among months, we used one-factor ANOVA. Mean values for fecundity and GSI were calculated by month of collection to examine trends in reproduction and peak spawning. One-factor ANOVA was used to test the null hypothesis that no significant difference existed in monthly fecundity (females). One-factor ANOVAs

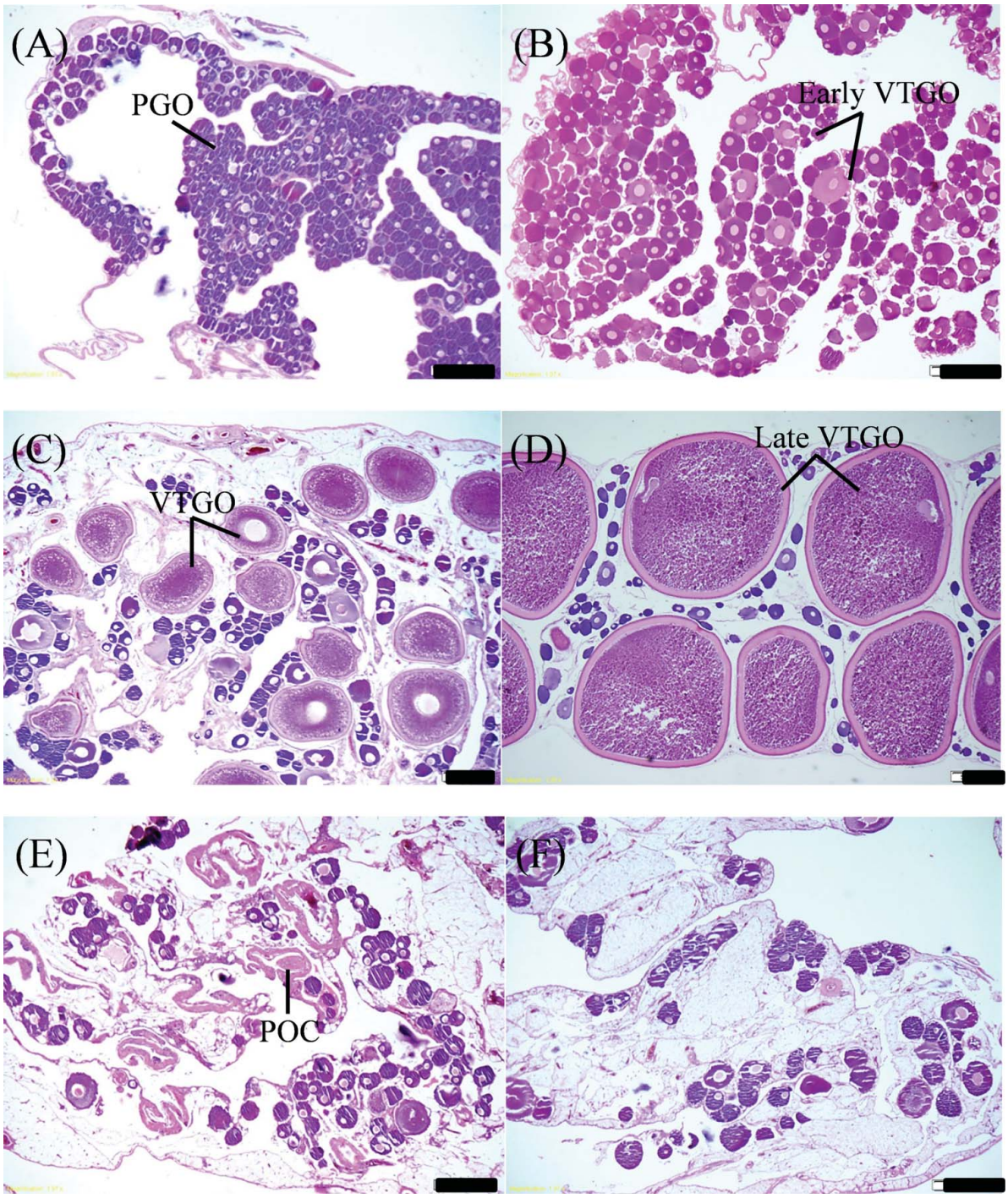

FIGURE 3. Reproductive histology of female Longnose Gars collected in the Charleston Harbor and Winyah Bay estuaries in South Carolina from May 2012 through July 2013. The panels show samples of gonad tissue from the following reproductive development stages: **(A)** immature, **(B)** early developing, **(C)** middle developing, **(D)** spawning capable, **(E)** regressing, and **(F)** regenerating. Abbreviations are as follows: PGO = primary growth oocyte, VTGO = vitellogenic oocyte, and POC = postovulatory complex.

were used to test the null hypothesis that no significant difference existed in monthly GSI (separate for females and males). Relative fecundity and GSI were log transformed ($\log_e X$) to meet the assumptions of normality and homogeneity of variance. Tukey's honestly significant difference tests were used to examine pairwise differences for each of the variables between months. The month with the significantly lowest values in fecundity and GSI was assumed to signal an end in peak

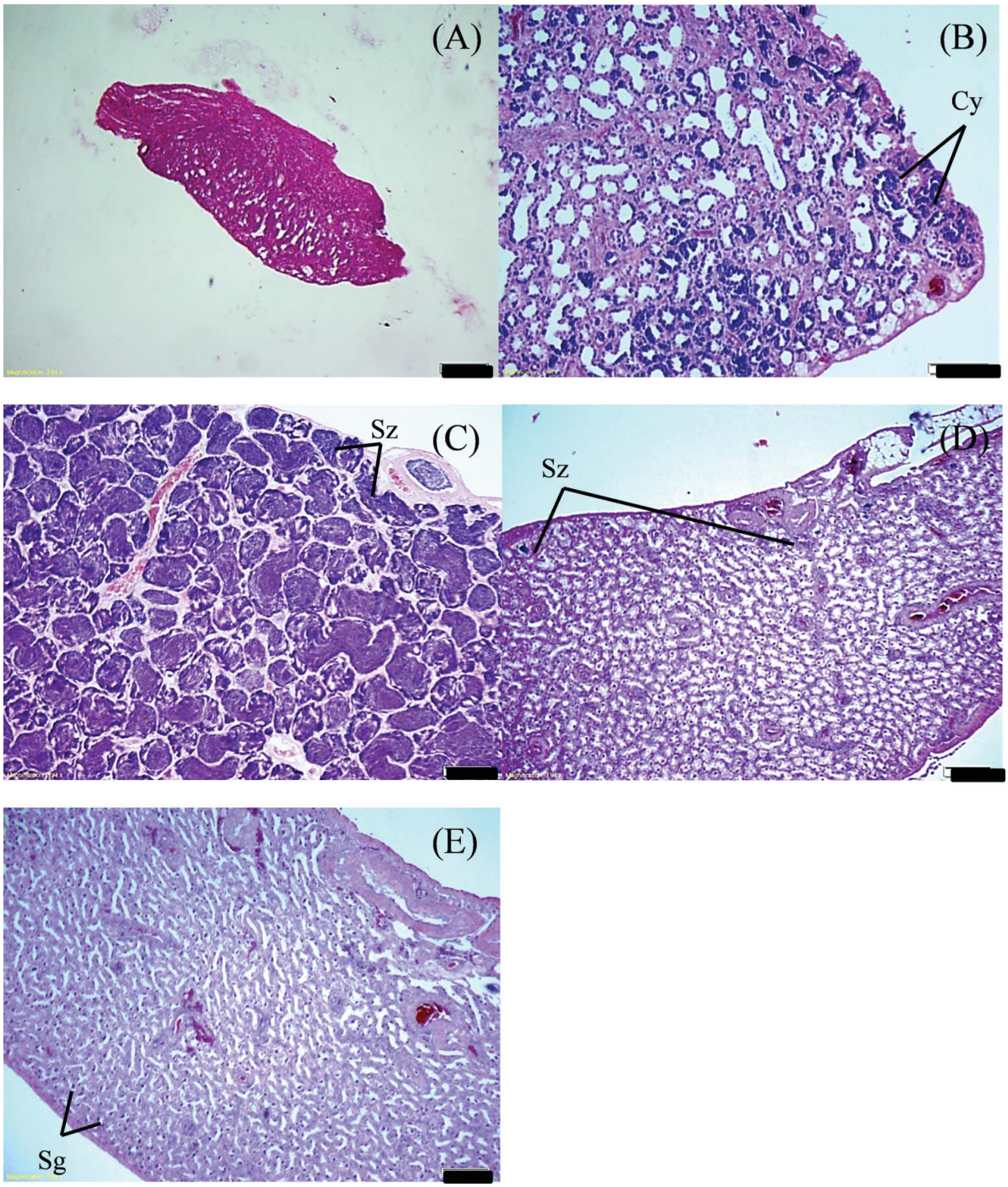

FIGURE 4. Reproductive histology of male Longnose Gars collected in the Charleston Harbor and Winyah Bay estuaries in South Carolina from May 2012 through July 2013. The panels show samples of gonad tissue from the following reproductive development stages: **(A)** immature, **(B)** developing, **(C)** spawning capable, **(D)** regressing, and **(E)** regenerating. Abbreviations are as follows: Cy = spermatocysts, Sz = spermatozoa, and Sg = spermatogonia.

spawning. Additionally, the percent of individuals assigned to each reproductive phase based on the month of collection were plotted separately for males and females to visually assess the spawning season duration and peak. Unless stated otherwise, data were analyzed using R. Results were considered significant when $P < 0.05$.

RESULTS

A total of 605 Longnose Gars were collected May 2012 through July 2013, ranging in size from 269 to 1,210 mm TL (Figure 6). Of these, 400 (269–1,210 mm TL) were collected from Charleston Harbor and 205 (472–1,018 mm TL) were collected from Winyah Bay. A total of 123 fish from Winyah

TABLE 1. Histological criteria, modified from Brown-Peterson et al. (2011) and Smith (2008). Primary, secondary, and tertiary vitellogenesis are indicated by Vtg1, Vtg2, and Vtg3, respectively.

Reproductive stage	Male	Female
Immature (never spawned)	Small testes, often threadlike. Only spermatogonia present; no lumen in lobules.	Small ovaries, blood vessels indistinct. Only oogonia and primary growth oocytes present. No atresia or muscle bundles. Thin ovarian wall and tightly packed oocytes.
Developing	Small testes. Spermatocysts along lobules. All stages (spermatocytes, spermatids, spermatozoa) of spermatogenesis can be present. No spermatozoa present in lumen of lobules or in sperm ducts. Germinal epithelium (GE) continuous throughout.	Early: Primary growth oocytes and cortical alveolar oocytes present. Early developed oocytes similar to cortical alveolar oocytes (in size) but have small, bright pink yolk vesicles forming a circle. Middle: Oocytes are larger and have substantially more yolk vesicles. Possess a pink, striated vitelline envelope. No oocytes beyond Vtg2.
Spawning capable	Large and firm testes. Presence of spermatozoa in lumen of lobules or sperm ducts. All spermatogenesis stages can be present. Spermatocysts throughout testis.	Large ovaries, blood vessels prominent. Individual oocytes visible macroscopically. Well-developed oocytes (Vtg3) present with thick vitellin envelopes, apparent early yolk coalescence, and nuclear migration. Postovulatory complexes may be present in batch spawners. Atresia of vitellogenic oocytes and early maturation may be present.
Regressing	Small and flaccid testes, no milt release with pressure. Residual spermatozoa present in lumen of lobules and sperm ducts. Scattered peripheral spermatocysts containing spermatocytes, spermatids, and spermatozoa. Little to no spermatogenesis. Peripheral spermatogonial proliferation and regeneration of GE common.	Flaccid ovaries, blood vessels prominent. Atresia (any stage) and postovulatory complexes present. Some cortical alveoli or vitellogenic (Vtg1, Vtg2) oocytes present.
Regenerating	Small testes. No spermatocysts. Lumen of lobule often nonexistent. Spermatogonia proliferation throughout testes and GE continuous. Few residual spermatozoa occasionally in lumen of lobules and sperm duct.	Small ovaries, blood vessels reduced but present. Only oogonia and primary growth oocytes present. Muscle bundles, enlarged blood vessels, thick ovarian wall and gamma or delta atresia or old, degenerating postovulatory follicles may be present. Appears similar to immature, but oocytes more dispersed and tissue appears loose.

Bay and 229 from Charleston Harbor were retained for the life history subsample, and these fish ranged in size from 269 to 1,199 mm TL. Electrofishing yielded 131 and 70 samples for Charleston Harbor and Winyah Bay, respectively, while trammel netting yielded 98 and 53. The size-frequency distribution of the subsample fish did not differ significantly from that of the total sample (Kolmogorov–Smirnov $Z = 0.08$; $P = 0.113$; Figure 6).

Age and Growth

Total weight (TW) increased proportionally with TL ($P < 0.001$). The length–weight model for males was $\log_e TW = 8.67281(\log_e TL) - 17.72861$ ($r^2 = 0.9827$), while females exhibited the following relationship: $\log_e TW = 8.79644 (\log_e TL) - 18.1585$ ($r^2 = 0.9816$). An ANCOVA revealed that this relationship did not differ significantly between the sexes ($P = 0.332$), and therefore the two sexes were combined into a

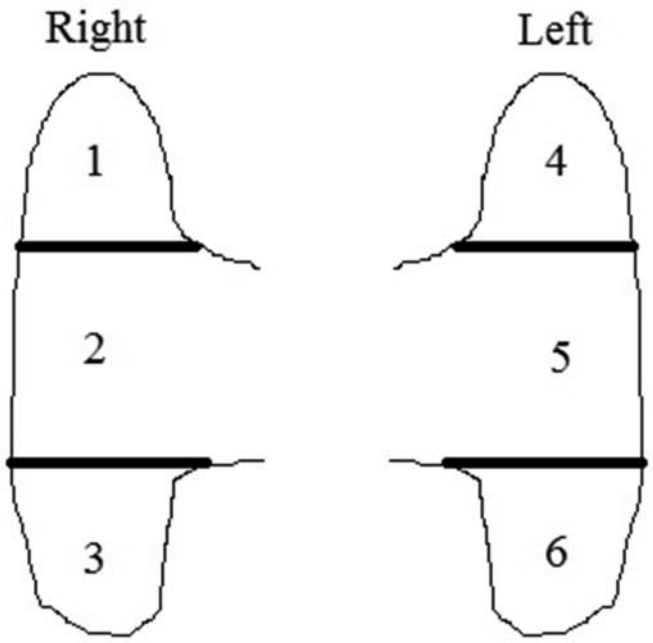

FIGURE 5. Subsample locations (1–6) within the ovaries for gravimetric fecundity estimation in Longnose Gars.

single length–weight model that yielded the following relationship: $\log_e TW = 3.74101(\log_e TL) - 17.60022$ ($r^2 = 0.9837$) (Figure 7). The size-frequency distribution of females was significantly larger than that of males ($Z = 0.46$, $P < 0.001$; Figure 8). Size frequency also differed between sampling sites ($Z = 0.26$, $P < 0.001$), with a wider range of sizes coming from Charleston Harbor. Additionally, larger sizes were collected from trammel netting than from electrofishing, which included many age-0 individuals ($Z = 0.45$, $P < 0.001$).

Annuli counts by the two readers were in exact agreement for 63% of the samples, within 1 year for 90% of the samples, and within 2 years for 99% of the samples. The average percent error between readers was low (3%). Overall, the estimated age for Longnose Gars ranged from 0 to 25 years. Female age ranged from 0 to 25 years with a mean ± SE of 9.0 ± 0.4 years, and males ranged from 0 to 17 years with a mean ± SE of 8.0 ± 0.3 years. The age-frequency distribution of females was significantly older than that of males ($Z = 0.18$, $P < 0.01$; Figure 9). Age frequency also differed among sampling sites ($Z = 0.22$, $P < 0.001$) due in part to a high number of age-0 individuals in Charleston Harbor, and younger samples were collected by electrofishing than by trammel netting ($Z = 0.5$, $P < 0.001$). The monthly proportion of otoliths with opaque edges increased from 0.1 in January to 0.4 in February, to 0.7 in March, and to 0.8 in April then declined in May to 0.5 and to 0.1 in June, indicating that increment formation occurred from February to May (Figure 10).

The two-stage least-squares regression of von Bertalanffy growth curves and growth parameters revealed that

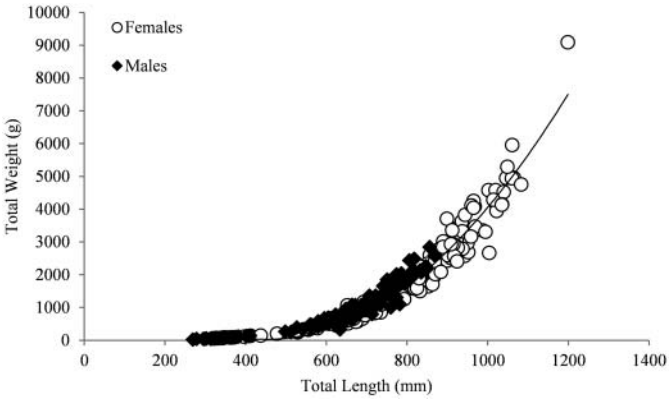

FIGURE 7. Relationship between total length and total weight for male and female Longnose Gars captured from Charleston Harbor and Winyah Bay, South Carolina, from May 2012 through July 2013.

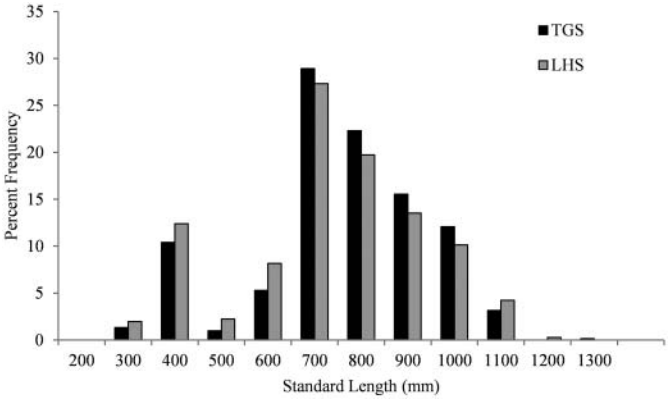

FIGURE 6. Size-frequency distribution of Longnose Gars collected from Charleston Harbor and Winyah Bay, South Carolina, from May 2012 through July 2013. Abbreviations are as follows: TGS represents the total gar sample and LHS represents the life history subsample.

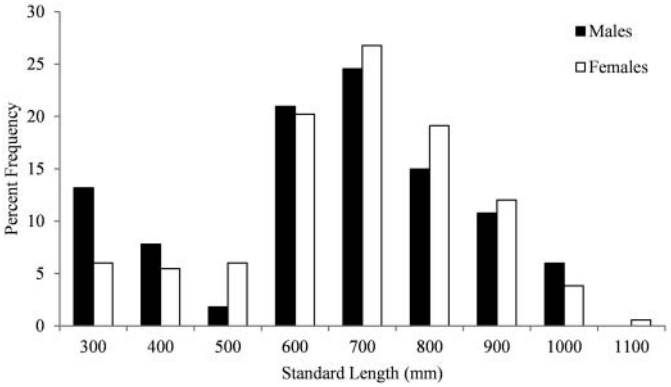

FIGURE 8. Frequency distributions for male and female Longnose Gars used in the life history subsample and captured in Charleston Harbor and Winyah Bay, South Carolina, from May 2012 through July 2013.

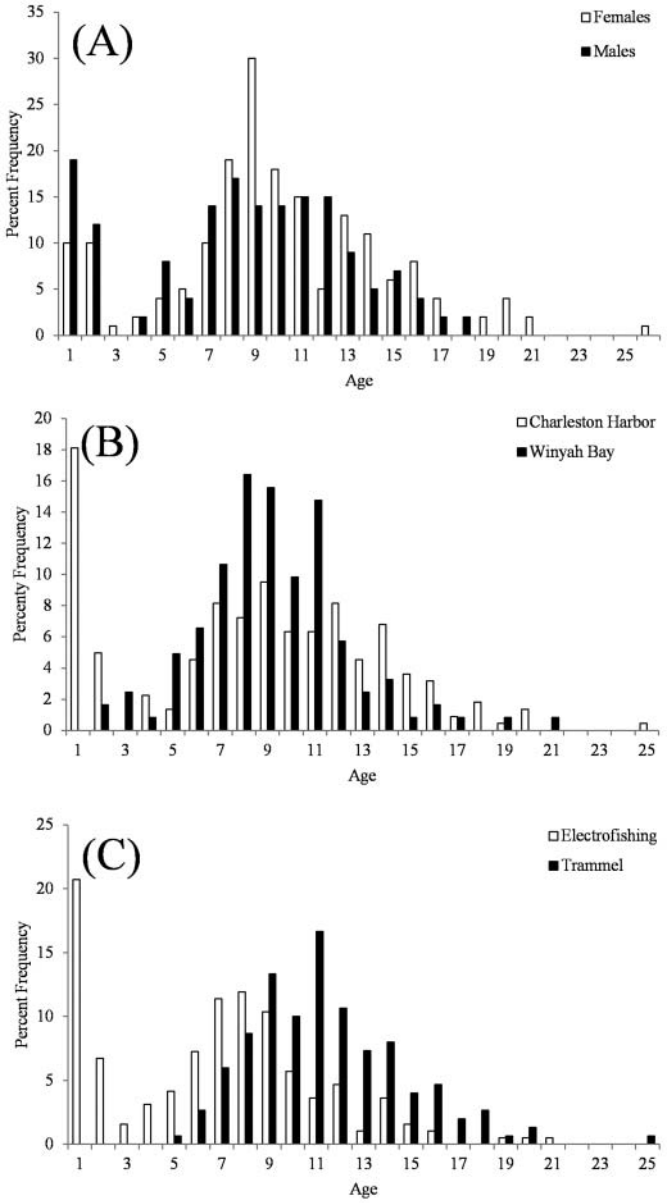

FIGURE 9. Age frequencies of Longnose Gars captured from May 2012 to July 2013. The histograms depict comparisons of **(A)** male and female samples, **(B)** samples collected from Charleston Harbor and Winyah Bay, and **(C)** samples collected by electrofishing and trammel netting.

size at age was significantly different between the sexes (age: $P < 0.05$; age × sex: $P < 0.05$). Tests of variance in length and age between males and females revealed that the variance in age was not significantly different ($P = 0.39$) but that variance in length was significantly different ($P < 0.05$), which indicated sexually dimorphic growth. The growth coefficient for males ($L_\infty = 739$, $K = 0.16$, $t_0 = -2.56$) was twice that of females ($L_\infty = 1{,}184$, $K = 0.08$, $t_0 = -3.45$; Figure 11), which was driven by the inverse relationship of L_∞ and K.

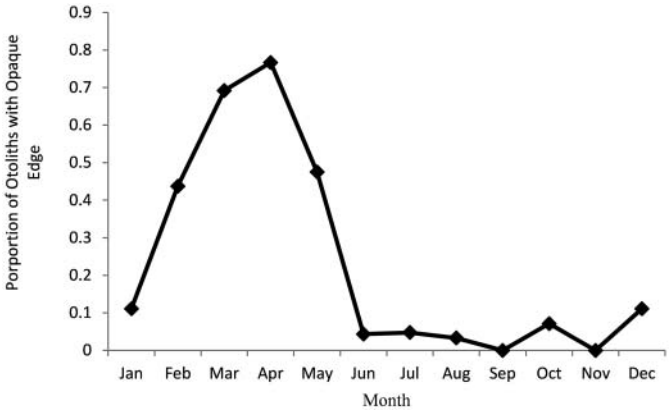

FIGURE 10. Proportion of otoliths with opaque edges by month for Longnose Gars caught from May 2012 through July 2013 in Charleston Harbor and Winyah Bay, South Carolina.

Reproduction

The overall sex ratio (female to male) was 1.09:1.00, but this was not significantly different from 1:1 ($\chi^2 = 0.65$, $P = 0.421$; Figure 12), and sex ratios did not significantly differ between estuaries ($\chi^2 = 0.41$, $P = 0.523$) or from 1:1 within individual estuaries (Charleston: $\chi^2 = 0.07$, $P = 0.789$; Winyah: $\chi^2 = 0.98$, $P = 0.321$). Between freshwater and salt water, sex ratios were significantly different ($\chi^2 = 5.44$, $P = 0.02$) but only in salt water did the sex ratio (1.41:1.00) differ from 1:1 (freshwater: $\chi^2 = 1.10$, $P = 0.294$; salt water: $\chi^2 = 4.98$, $P = 0.026$). By length, 50% of males were mature at 301 mm TL and 50% of females were mature at 506 mm TL (Figure 13). By age, 50% of males were mature at 1.0 year of age and 50% of females were mature at 5.6 years of age (Figure 14).

Early developing females were seen in 10 out of 12 months, with the greatest proportion of developing individuals collected in June (Figure 15A). Primary growth, cortical alveolar,

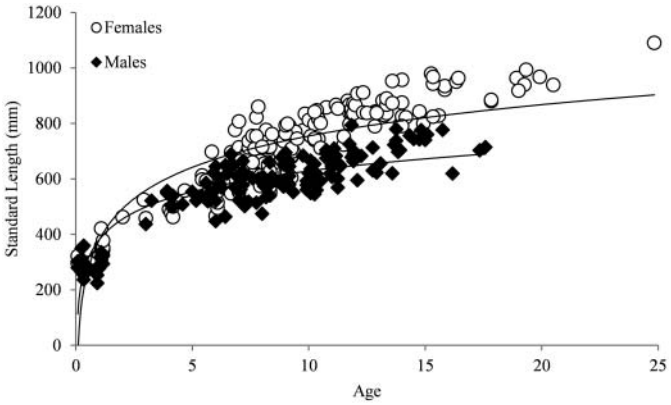

FIGURE 11. Length at fractional age for male and female Longnose Gars collected from Charleston Harbor and Winyah Bay, South Carolina, from May 2012 through July 2013. The curves are logarithmic.

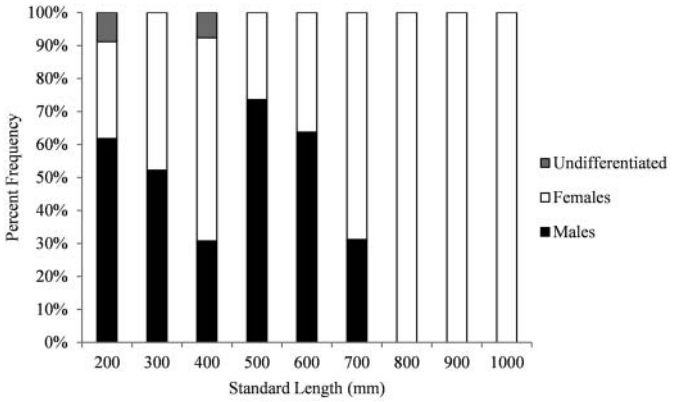

FIGURE 12. Percent frequency of each sex relative to the total length for Longnose Gars from Charleston Harbor and Winyah Bay, South Carolina, captured from May 2012 through July 2013.

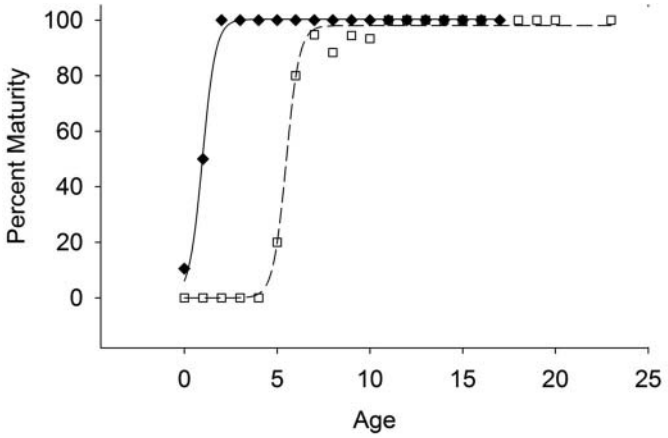

FIGURE 14. Percent maturity at age for male (black diamonds, solid line) and female (white squares, dashed line) Longnose Gars captured in Charleston Harbor and Winyah Bay, South Carolina, from May 2012 through July 2013.

and vitellogenic oocytes were documented throughout the year. Spawning-capable females were collected in every month except July at which time the GSI decreased to its lowest value of the year, indicating that the spawning season had ended. The proportion of regressing females was highest from May through July while the frequency of spawning-capable females declined during this time period as well (Figure 15A). Spawning-capable males were collected in all months, and the proportion of regressing males increased during the summer and early fall (Figure 15B). Male development was documented primarily in summer and fall while regressing males were collected at different times of the year. Male GSI peaked in October and remained fairly constant until March, then declined through July. From April to July, spawning-capable males and females were rarely captured in saline waters and females in this stage were found almost exclusively in the headwaters of the Ashley River, indicating that spawning occurred during this time and in freshwater. Headwaters in Winyah Bay were not sampled.

Potential annual fecundity averaged 21,988 oocytes (SE = 2,037; $n = 55$), with a range of 1,296–86,009 oocytes. No bias in estimation was detected based on subsample location within the ovary (df = 55, $P = 0.225$). Fecundity was positively

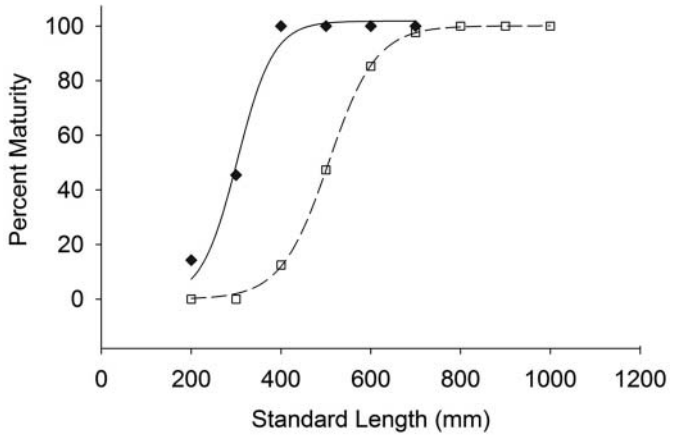

FIGURE 13. Percent maturity by length for male (black diamonds, solid line) and female (white squares, dashed line) Longnose Gars captured in Charleston Harbor and Winyah Bay, South Carolina, from May 2012 through July 2013.

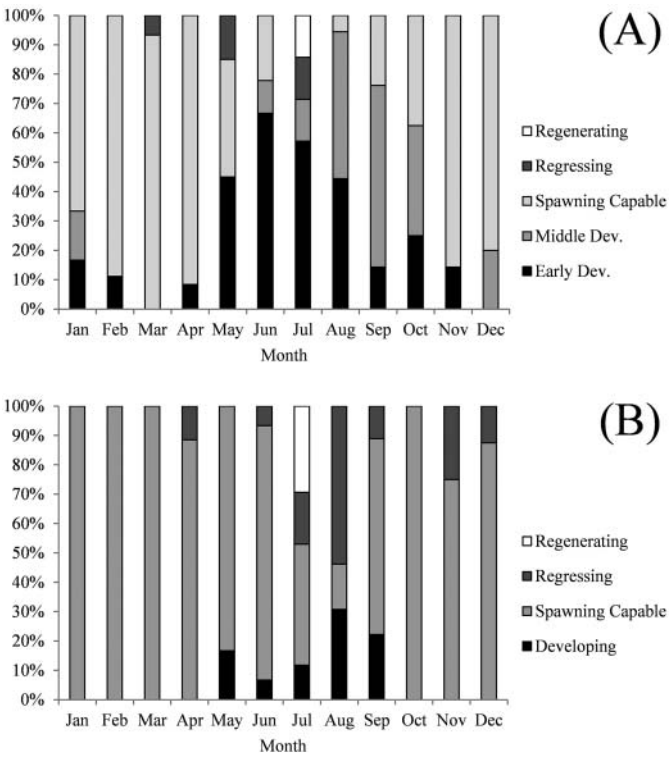

FIGURE 15. Percentage of each reproductive stage by month for **(A)** female and **(B)** male Longnose Gars captured from May 2012 through July 2013 in Charleston Harbor and Winyah Bay, South Carolina; Dev. = developing.

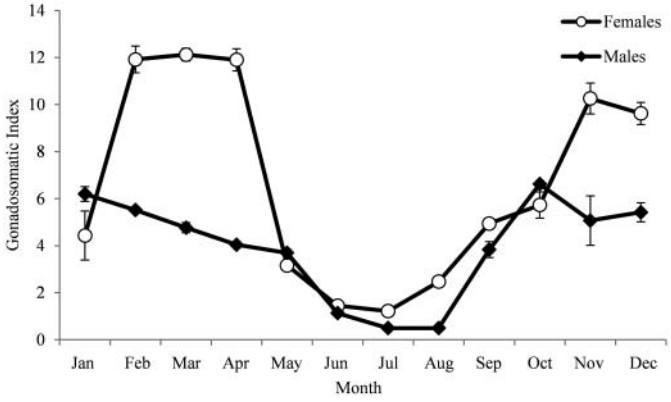

FIGURE 16. Mean monthly gonadosomatic index for mature Longnose Gars captured from Charleston Harbor and Winyah Bay, South Carolina, from May 2012 through July 2013. The error bars represent the standard error.

correlated with total weight ($R^2 = 0.870$, $P < 0.001$) and standard length ($R^2 = 0.730$, $P < 0.001$). Among months, fecundity was not significantly different but only marginally so (ANOVA: df = 6, $F = 1.949$, $P = 0.09$). However, there was a significant difference in fecundity between March and May (Bonferroni: $P < 0.01$). Mean ± SE relative fecundity was 67 ± 2 oocytes/g body weight ($n = 55$) and did not differ significantly among months (ANOVA: df = 6, $F = 0.98$, $P = 0.45$). The GSI varied significantly among months for females (ANOVA: df = 11, $F = 8.851$, $P < 0.001$) and males (ANOVA: df = 11, $F = 6.9$, $P < 0.001$; Figure 16). The GSI in mature females peaked in March at 15.16 ± 1.43 (mean ± SE) and was at a minimum in July at 1.33 ± 0.23 (Figure 16); in mature males it was highest in October at 7.61 ± 0.45 and lowest in July at 0.51 ± 0.13.

DISCUSSION

Age and Growth

Longnose Gars were relatively abundant in the two estuarine systems we examined. A study in Florida reported a range expansion for Longnose Gars, despite a decline in numbers in some parts of their historic range, due to canals providing conduits to previously uninhabited areas in the southern part of the state (Gandy et al. 2012). In coastal South Carolina estuaries, Longnose Gar abundance has remained relatively stable over the past decade (SCDNR, unpublished monitoring data) and they are the sixth most abundant species collected by the SCDNR Inshore Fisheries monitoring efforts (C. J. McDonough, unpublished data).

The current study is unique in that we utilized sectioned sagittal otoliths for estimating age. Branchialstegal rays have been traditionally used to age gar species; however, many studies have shown that otoliths provide more reliable estimates of age than do other structures, especially for older individuals (Erickson 1983; Barber and McFarlane 1987; Nash and Irwin 1999; Buckmeier et al. 2012). Buckmeier et al. (2012) reported that only the otoliths of Alligator Gar *Atractosteus spatula* provided accurate age estimates of known-age and chemically marked fish when compared with commonly used external aging structures like fin rays and scales. The other structures examined underestimated age and overestimated growth. Similar findings have been reported for other freshwater fish species (Erickson 1983; Buckmeier et al. 2002; Maceina and Sammons 2006). Branchialstegal rays may underestimate the age of older fish because they become opaque with age and early annuli may erode with time (Ferrara 2001; Brinkman 2003). In our study, marginal increments formed around April. Among other species within the region, Vermilion Snapper *Rhomboplites aurorubens* in the South Atlantic Bight formed annual increments in June (Zhao et al. 1997; Potts et al. 1998), Southern Kingfish *Menticirrhus americanus* formed increments between March and July (Smith and Wenner 1985), and in two South Carolina studies, Bluegill *Lepomis macrochirus* and Striped Mullet *Mugil cephalus* formed increments from April to May and in July, respectively (Hales and Belk 1992; McDonough et al. 2005). In the Gulf of Mexico, Alligator Gars formed increments around May (Buckmeier et al. 2012). Each of these studies found annual increments to form around the same time of year as the present study, which adds confidence to the use of sectioned otoliths as an aging structure.

A few studies have reported age and growth in Longnose Gars across a range of locations and ecosystems (see Supplementary Tables S.1 and S.2 available in the online version of this article). The maximum reported ages for male and female Longnose Gars are 22 and 27, respectively, and these were determined using branchialstegal rays in coastal Virginia (McGrath 2010). The maximum reported lengths are 1,092 mm TL for males (Johnson and Noltie 1996) and 1,379 mm TL for females (Ferrara 2001). In the present study, a wider range of sizes was captured in Charleston Harbor than in Winyah Bay and larger sizes were captured by trammel netting than by electrofishing. Age frequency was younger in low-salinity waters, where electrofishing was employed, which is likely due to a dominance of young-of-the-year individuals. Age frequency was also younger in the Charleston Harbor site, where many more age-0 individuals were collected than in Winyah Bay. These findings suggest that age-0 Longnose Gars are generally found in low-salinity waters while larger and older individuals reside further downriver.

The current study documented similar maximum ages for males and females to the other coastal study (McGrath 2010), although different aging structures were used and maximum fish size was smaller in South Carolina. Direct comparisons among studies are difficult because of differences in sampling

design and interpretation of increments. However, one reason for the differences in maximum ages reported across the range of studies may relate to the sample size of fish examined within each study (Table S.1). The one freshwater study with a relatively large sample size (Ferrara 2001: 187 fish) may have underestimated the maximum age because it used whole otoliths and newer increments may have been obscured and therefore undetected. Studies on other fish species have documented that one disadvantage to using whole otoliths in age estimation is that they tend to underestimate age (Beamish 1979; Sipe and Chittenden 2002). Differences in mean and maximum ages from the various studies could also relate to differences in the aquatic habitats sampled. The two coastal studies documented the maximum ages reported for this species. Further investigations comparing riverine, estuarine, and reservoir gar populations are necessary to determine if habitat-related differences in age structures exist.

In addition to the current study, four studies provided growth information for Longnose Gar populations (Table S.2). Differences in growth estimates could be related to differences in sampling design, sample sizes, aging structures used, habitats and locations sampled, or a combination of these factors, which makes only qualitative comparisons of the von Bertalanffy parameter estimates possible. One factor in particular could have been the relative proportional number of younger, smaller individuals in each study. Higher numbers of these younger, smaller individual specimens would result in lower L_∞ values and differing growth coefficients. However, all but one of these studies were in agreement with this study in that significant differences in growth occurred between male and female Longnose Gars and that growth should be modeled separately by sex (Ferrara 2001; McGrath 2010; Kelley 2012).

Reproduction

While the present study on Longnose Gars did not find an overall sex ratio different from 1:1, other studies have reported a deviation from this ratio, which may have been related to low sample size (Ferrara 2001) or sampling bias (Love 2004). Several possible explanations exist that may explain the female-dominated sex ratio seen in saltwater regions in the current study. One reason could relate to the differences in the energetic requirements between the sexes and locational differences in energy-rich prey items. For example, Atlantic Menhaden *Brevoortia tyrannus* are more common in higher salinities (Nelson et al. 1991) and are a common prey item of Longnose Gars (Klaassen and Morgan 1974; Henzler 2011; McGrath et al. 2013). Klaassen and Morgan (1974) found that locational differences in growth rate may be attributed to the relative abundance of Gizzard Shad *Dorosoma cepedianum*, another common Clupeid. Female gars have larger body sizes and greater energetic investment into reproduction than male conspecifics, which may encourage the females to stay in regions where energy-rich prey, such as Atlantic Menhaden, are abundant. Habitat use and movement patterns of this species remain largely unstudied, requiring further research.

Gear selectivity may have also potentially resulted in the female-dominated sex ratio found in salt water because trammel nets select for larger animals based on the mesh size. Females grow to larger body sizes than males, which may result in higher capture rates of females proportional to males in regions where trammel nets are employed.

No published accounts of length at maturity were found for comparison; however, some information for age at maturity was found. In the current study, 50% maturity for males was approximately 2 years earlier than that found in the previous studies but for females it was at approximately the same age as in the other studies (Table S.3; Netsch and Witt 1962; Johnson and Noltie 1996; Ferrara 2001; McGrath 2010). The earlier time to maturity in male Longnose Gars in the current study compared with previous studies could be driven by environmental forces influencing maturation rate, could be the result of inconsistency in aging methods among studies, or could reflect that morphological determinations of sexual maturity underestimate the true number of mature individuals. The use of different aging structures can produce substantially different age estimates, which in turn affects the estimated age at which maturity is reached, though additional research is necessary to determine if that is the case among studies on Longnose Gars. Age at maturity was determined using a logistic regression, which can be influenced by the number of small fish or immature fish included in the calculation and by whether the samples are representative of the population.

Reproductive histology has only been employed in lepisosteids a few times (Orlando et al. 2007; Smith 2008) and never in Longnose Gars prior to the present study. Development for spawning was seen throughout the year, but the proportion of developing females, the degree of development, and the GSI substantially increased in early fall. Oocytes attained morphological traits of spawning-capable oocytes, including migration of the nucleus to the animal pole and early yolk coalescence, during autumn, but the presence of postovulatory follicles, indicating recent spawning, were not found to occur until spring. Smith (2008) hypothesized that Spotted Gars retained their spawning-capable oocytes for extended periods until the oocytes reached a threshold size, which may also be true for Longnose Gars. Male GSI was highly variable but generally increased in the fall and winter, followed by a gradual decline in spring and summer. While no spawning events were witnessed in this study, histology and the GSI suggested that spawning occurred from late April through May. This agreed with the findings of another study on reproduction in tidally influenced Longnose Gars in South Carolina by Henzler (2011). The timing of spawning varies by location in this species and may depend on latitude and the primary productivity of the spawning location (Netsch and Witt 1962; Henzler 2011) (Table S.4). Several reports

have proposed that gars move upstream to spawn (Netsch and Witt 1962; McGrath 2010), a hypothesis that is supported in the current study by the lack of spawning-capable individuals in saline waters and the presence of regressing females with postovulatory complexes in Charleston Harbor headwaters during the months of spawning.

At any given time, two cohorts of oocyte stages were found: (1) primary growth oocyte and cortical alveolar oocyte stages and (2) large, vitellogenic oocytes to be spawned in the upcoming spawning season. This development strategy is typical of group-synchronous fishes (Murua and Saborido-Rey 2003; Brown-Peterson et al. 2011). Additionally, the clear distinction in oocyte size between the two clutches indicates that this species exhibited determinate fecundity (Hunter et al. 1992) as oocytes did not appear to be continually recruited throughout the development season. In addition, females that had recently spawned, as evidenced by the presence of postovulatory complexes, often retained many well-developed oocytes, which suggests that Longnose Gars may spawn their total annual allotment of developed oocytes in several batches over a relatively short time period. Additional samples of actively spawning individuals are necessary to determine the frequency of spawning. This reproductive strategy is similar to what has been described for Spotted Gars (Smith 2008). Smith (2008) described the Spotted Gar reproductive strategy as exhibiting group-synchronous oocyte development and spawning the vitellogenic oocytes in batches over a short period of time, though this study lacked regressing individuals and therefore spawning periodicity is unclear. Orlando et al. (2007) also described a similar strategy for Florida Gar *Lepisosteus platyrhincus*, which display group-synchronous development and therefore could potentially spawn repeatedly (in batches) during the spawning season, but no evidence of this was found (Table S.4). According to Murua and Saborido-Rey (2003), batch spawners are fishes that release vitellogenic oocytes in clutches over a span of days to months, while Brown-Peterson et al. (2011) define batch spawners as fishes that release multiple clutches of vitellogenic oocytes throughout the spawning season. Based on these definitions, it is likely that Spotted, Longnose, and Florida gars all exhibit a reproductive strategy characterized by group-synchronous development and the release of all vitellogenic oocytes in batches over a very short period of time. Aside from lepisosteids, sturgeons (family Acipenseridae) are late to mature, exhibit long ovarian development cycles, and have large (>3 mm in diameter) oocytes similar to gars. A histological examination of White Sturgeon *Acipenser transmontanus* revealed that previtellogenic oocytes persisted following spawning, which may be an indication of group-synchronous development, though spawning periodicity within a spawning season was not described (Doroshov et al. 1997).

Like in most fishes, fecundity was positively correlated with body size. This study's average fecundity of 21,988 oocytes was slightly lower than that found in other Longnose Gar studies (Table S.4), which could be explained by the positive relationship between female size and fecundity and the capture of smaller females in this study compared with the other studies.

This study provides the first comprehensive description of age, growth, and reproduction of Longnose Gars by employing reproductive histology for this species and is one of a few life history studies on Longnose Gars within a coastal environment. Longnose Gars are ubiquitous in freshwater and estuarine systems in the eastern United States, represent a substantial proportion of biomass in these habitats, and are top predators. Therefore, more research is needed to further illuminate the basic biology and ecological role of this species.

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