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ARTICLE

Gray Triggerfish Reproductive Biology, Age, and Growth off the Atlantic Coast of the Southeastern USA

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Abstract

The Gray Triggerfish *Balistes capriscus* supports fisheries on both sides of the Atlantic Ocean. We utilized fishery-independent samples to assess the age structure, growth, sex ratio, size and age at maturity, spawning season, and spawning frequency of the Gray Triggerfish population off the southeastern U.S. Atlantic coast. From 1991 to 2012, 7,685 samples were collected, ranging in FL from 82 to 578 mm and ranging in age from 0 to 13 years. Our study provides key life history information for an exploited population and is the first to comprehensively describe age, growth, and reproduction for a *Balistes* species. We documented that the Gray Triggerfish is sexually dimorphic, with adult males attaining larger sizes at age and a larger maximum size than females. Sex-specific growth curves were fitted, yielding the following von Bertalanffy equations: $FL_t = 419[1 - e^{-0.54(t + 0.61)}]$ for males and $FL_t = 352[1 - e^{-0.94(t + 0.22)}]$ for females. This species is characterized by a medium size at maturity (the smallest mature female was 179 mm FL; the smallest mature male was 183 mm FL) and relatively early age at maturity (the youngest mature female and male were age 0). Some shifts in population attributes coincided with a period of increased fishing pressure. Due to tighter regulations on snapper and grouper fisheries, the Gray Triggerfish has become a more targeted species. Fisheries biologists and managers should continue to evaluate potential impacts and establish management regulations that consider the region-specific reproductive season, size and age at maturity, and sex-specific differences in growth documented in this study.

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Triggerfishes (Family Balistidae) occur in almost all the major oceans (Matsuura 2015). Species from the genus *Balistes* support productive fisheries in the Pacific Ocean and throughout the Atlantic Ocean, north and south of the equator (Bernardes 2002; Barroso-Soto et al. 2007; NMFS 2009; Aggrey-Fynn and Sackey-Mensah 2012), and into the Mediterranean Sea (Kacem and Neifar 2014; Kacem et al. 2015), the Gulf of Mexico (SEDAR 2006), and the Caribbean Sea (Matos-Caraballo 2012; SEDAR 2013). Effective fisheries management requires a detailed understanding of the life history strategies of managed species (Chale-Matsau et al. 2001; King and McFarlane 2003); however, little published information exists on the reproductive biology, age, and growth of *Balistes* spp.

The Gray Triggerfish *Balistes capriscus* is a moderately long-lived species that is associated with hard-bottom habitat along the eastern and western coasts of the Atlantic Ocean and supports fisheries from as far north as the Mediterranean (Kacem and Neifar 2014), as far south as Brazil (Bernardes and Dias 2000), and along both Atlantic coasts (SEDAR 2006; Aggrey-Fynn 2013). Individuals of this species spend some time in the water column as juveniles, when they are associated with *Sargassum* spp. (Ingram 2001; Wells and Rooker 2004; Casazza and Ross 2008); eventually, they settle into a more benthic existence and are most commonly associated with natural and artificial reefs, rocky outcroppings/hard bottom, and wrecks. Adult Gray Triggerfish feed diurnally on invertebrate prey, such as mollusks, crustaceans, and echinoderms (Frazer et al. 1991; Vose and Nelson 1994; Blitch 2000).

Gray Triggerfish exhibit a relatively unusual mating strategy in comparison with other medium-sized reef fishes that are targeted by fisheries. Harem-like reproductive behavior has been observed in which males construct demersal nests and perform courtship behaviors (e.g., they change color and circle the females) to attract multiple females with which to mate (Simmons and Szedlmayer 2012). After fertilization, parental care of the demersal eggs by both sexes has been observed. Typically, a female stays inside the nest and guards the eggs, while the male guards the territory surrounding the nests. These behaviors continue until the eggs hatch, which occurs within 24–48 h after fertilization (Simmons and Szedlmayer 2012).

Commercial and recreational fisheries target Gray Triggerfish in the Mediterranean (Kacem et al. 2015), U.S. Atlantic (North Carolina through Florida), U.S. Gulf of Mexico (SEDAR 2006), Brazil (Bernardes and Dias 2000), and Africa (Aggrey-Fynn and Sackey-Mensah 2012). Fishing pressure in the USA is relatively high, as the Gray Triggerfish is one of the top-10 species in terms of average landings (by weight) within the South Atlantic Fishery Management Council's snapper–grouper management complex (unpublished data source cited by Burton et al. 2015). Historical commercial and recreational annual landings for Gray Triggerfish in this area increased from near 0 kg in the 1970s to a peak of nearly 200,000 kg in the mid-1990s, declined to around 90,000 kg in the early 2000s, increased to over 200,000 kg in 2012, and continue to remain high (NMFS Sustainable Fisheries Branch 2014a, 2014b; Burton et al. 2015). Fishery-independent abundance indices have highlighted a corresponding decline in overall population numbers during 2002–2011 (Figure 1). The Gray Triggerfish continues to be an important fisheries species in this region.

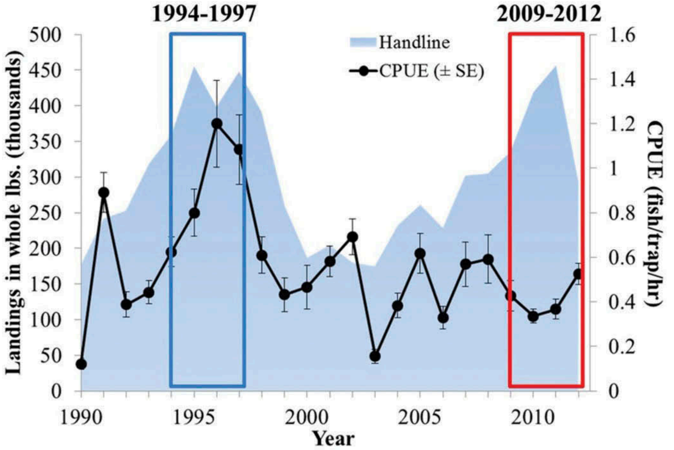

FIGURE 1. Commercial landings of Gray Triggerfish (thousands of pounds; 1 lb = 0.454 kg) represented by handline data (the predominant commercial fishery gear for capturing this species) and standardized CPUE (fish·trap^{-1}·h^{-1}; ±SE) of Gray Triggerfish in chevron traps (reported by Ballenger et al. 2013) off the southeastern U.S. Atlantic coast from 1990 to 2012. Rectangles indicate the two periods of interest in the present study: 1994–1997, representing a peak in commercial landings and CPUE; and 2009–2012, representing another peak in commercial landings but a relatively low CPUE.

Several published studies have reported that intense fishing pressure appears to elicit changes in the life history patterns of marine fisheries species (Jørgensen 1990; Harris and McGovern 1997; Morgan and Colbourne 1999; Hunter et al. 2015). Currently, there is no published comprehensive life history study that has described age, growth, and reproduction in Gray Triggerfish or any *Balistes* species. The purpose of the present study was to utilize fishery-independent samples to assess the age structure, growth, sex ratio, size and age at maturity, spawning season, and spawning frequency of the Gray Triggerfish population off the southeastern U.S. Atlantic coast.

METHODS

Fish collection and processing.—Gray Triggerfish were collected through (1) the fishery-independent Southeast Reef Fish Survey (SERFS) by the Marine Resources Monitoring, Assessment, and Prediction Program (MARMAP) and the Southeast Area Monitoring and Assessment Program–South Atlantic at the South Carolina Department of Natural Resources (SCDNR) and (2) the Southeast Fishery-

Independent Survey conducted by the National Marine Fisheries Service's (NMFS) Southeast Fisheries Science Center. Fish were obtained with chevron traps from 1991 to 2012 and were processed for analyses of age and reproduction (*n* = 7,685). Chevron traps (Collins 1990) were deployed during daylight hours in depths ranging from 10 to 110 m at sites that were randomly chosen from a universe of known locations of natural reef habitat (live bottom and rocky ledges). From 1991 to 2012, approximately 2,500 live-bottom sites were included, from which 300–900 randomly chosen sites were sampled annually. Traps were baited using whole and cut clupeids (mainly menhaden *Brevoortia* spp.) and remained in the water for approximately 90 min. Depth, latitude, longitude, sampling duration, and time of collection were recorded for each trap set. Once removed from the traps, Gray Triggerfish specimens were weighed to the nearest gram and measured for SL, FL, and TL to the nearest millimeter.

The overall period in which we sampled Gray Triggerfish for this study was 1991–2012. Additionally, based on abundance trends combined with fisheries landings (Figure 1), we selected two shorter time periods for comparative purposes in examining life history trends. The additional time periods were (1) 1994–1997, during which Gray Triggerfish landings peaked and the fishery-independent abundance index indicated a peak in the population; and (2) 2009–2012, when fisheries landings peaked again, but the fishery-independent abundance index indicated a decline in population numbers.

To determine whether the population size structure of Gray Triggerfish changed between the two periods, we used two separate Kolmogorov–Smirnov (K–S) tests (one for males and one for females) to evaluate the null hypothesis that the size structure of fish collected during 1994–1997 did not differ from that of fish collected in 2009–2012. We also used K–S tests to examine for significant differences in the size frequency distribution between males and females within each time period (1991–2012; and the two shorter periods, 1994–1997 and 2009–2012). To assess whether mean size significantly differed between males and females and between the two time periods, we utilized a two-factor ANOVA with size (FL) as the dependent variable and with time period and sex as the independent factors.

For our evaluation of whether fish size was correlated with depth of capture, a subset of fish size data was selected by using four conditions: (1) to control for possible long-term shifts in the population's size structure, we only used data from 2004 to 2012; (2) to control for latitudinal-related water temperature trends, we established two main areas of interest (a North Carolina area from 33°N to 35°N and 76°W to 78°W; and a South Carolina area from 32°N to 33°N and 79°W to 80°W); (3) we selected data from two discrete depth zones (<36 m and 40–65 m) so that size distributions could be compared; and (4) considering that the main sampling efforts conducted by SERFS occurred during May–September, only samples from those months were used in the analyses. For each area, we tested the following two null hypotheses: (1) male or female sizes do not differ with depth of capture based on linear regression analyses; and (2) male or female size frequency distributions do not differ between the two depth zones based on K–S tests.

Statistical analyses were conducted in SPSS (IBM 2012) and RStudio (RStudio Team 2013), and the results were considered significant at *P*-values less than 0.05. If assumptions for statistical tests were not met, then the data were log transformed.

*Age and growth.—*The first dorsal spine is currently the accepted structure for estimating age in Gray Triggerfish (Moore 2001; Fioramonti 2012). The spine was removed from the fish, cleaned of excess tissue, and stored dry until further processing. Two sections immediately distal to the condyle groove were cut from each spine (0.5–0.7-mm thickness) by using a low-speed saw with a diamond-edged blade. The sections were then mounted on glass slides with a clear mounting medium and were viewed under a dissecting microscope at 10–20× magnification using transmitted light. Increment count was determined by identifying and enumerating the pattern of faster-growing (opaque) and slower-growing (translucent) zones that were assumed to represent 1 year of peak growth and slow growth seasons.

Fish age was estimated for each spine section by counting the number of translucent zones. Multiple readers estimated ages for fish collected during 1994–1997 and 2009–2012. At least two independent readers evaluated increments on a spine section without knowledge of the fish's length or date of capture. For this study, increment counts were considered age estimates. However, age validation of the first dorsal spine has not been performed for this species. Spine sections for which reader disagreement occurred were re-evaluated simultaneously by both readers, and a consensus count was recorded as the final age estimate in whole years. Other studies have reported low between-reader precision for age estimates based on Gray Triggerfish spines (Fioramonti 2012; Burton et al. 2015). Therefore, we assessed reader precision by using the same methods so that precision estimates could be compared among studies. Between-reader precision was estimated by calculating percent agreement between readers for perfect agreement and for agreement within ±1 year. We also computed the average percent error (APE) for age estimates between readers (Beamish and Fournier 1981).

Spine section margins were evaluated as either containing the final translucent zone along the edge or containing the final opaque zone. Using age-3, age-4, and age-5 fish collected from 2009 to 2012, we estimated the timing of increment formation by examining the monthly proportion of spines with translucent zones at the spine edge. This allowed for a reasonable approximation of increment periodicity, if not a full validation. Fractional age estimates were calculated based on the date of capture and the presumed birth date of July 1, which took into account the period of translucent band deposition and the peak of the spawning season.

For the 2009–2012 period, we compared the age frequency distributions between males and females by using a K–S test to determine whether age structure differed between the sexes. A Student's *t*-test was used to examine for significant differences in mean age between males and females within the current (2009–2012) period.

Von Bertalanffy growth curves (von Bertalanffy 1938) fitted to observed lengths at age for males and females sampled during 2009–2012 were used to determine the growth rates exhibited by the current Gray Triggerfish population. To provide a more representative estimate of von Bertalanffy growth parameters within the population off the southeastern U.S. Atlantic coast, we included 12 newly settled juvenile Gray Triggerfish that were collected from *Sargassum* spp. off the South Carolina coast during 2011–2014 and processed for sex and age determination. Growth curve parameters were compared between sexes by using analysis of residual sums of squares (RSS; Chen et al. 1992).

Reproduction.—Gonads were removed from the fish; the posterior portion of each gonad was fixed in an 11% solution of seawater-buffered formalin for up to 2 weeks and then was transferred to a 50% solution of isopropanol. Gonad samples were processed by using standard histological procedures (Harris and McGovern 1997; Wyanski et al. 2000; Harris et al. 2007). The tissue samples were vacuum-infiltrated and blocked in paraffin wax. Three transverse sections (~7 μm thick) were cut using a rotary microtome, mounted on glass slides, stained with double-strength Gill hematoxylin, and counterstained with eosin-y.

Stained sections were viewed under a compound microscope to determine the individual's sex and its reproductive phase, which was assessed according to a modified version of the histological criteria utilized in previous reef fish studies (Table 1; Supplementary Figures S.1–S.3 available in the online version of this article) and with slight modification in terminology for consistency (Brown-Peterson et al. 2011). Two readers independently assigned sex and reproductive phase without knowledge of the date of capture, specimen length, or specimen age. If differences in assignments of reproductive phase occurred, the readers examined the slide simultaneously to attempt a consensus assignment. If no consensus was reached, that specimen was eliminated from the analyses. During this process, we noted that the gonads of male Gray Triggerfish were unique in their structure and function compared to other species in the snapper–grouper management complex (Figures S.1, S.2), so we documented the male gonad structure and its relevance to determining reproductive phase as part of this study (Figure S.2).

To ensure that specimens in the immature and resting phases were assigned correctly, the size frequency of fish that were definitely mature (i.e., developing, spawning capable, or regressing) was compared to the size frequencies of immature fish and regenerating fish. Individuals of uncertain sex or reproductive phase were excluded from this analysis. If little or no overlap in FL was observed for immature and regenerating specimens, then we assumed that the phases were assessed correctly.

Spawning activity in females was denoted by the presence of oocyte maturation and postovulatory follicle complexes (POCs; Figure S.3). The POC stages were assigned based on the level of degeneration present in the POC in accordance with Moore (2001). The spawning season was defined as extending from the first date when late oocyte maturation or POCs were observed in a specimen to the latest date when POCs were present in a specimen. Stage-1 POCs showed little degeneration, large size, distinct thecal and granulosa layers, and a highly convoluted lumen. Stage-2 POCs were smaller than stage-1 POCs, showed degeneration of the granulosa and thecal layers, and presented a less-distinct lumen relative to stage-1 POCs. Stage-3 POCs exhibited a characteristic triangular shape of the granulosa layer, a loss of most granulosa cells, further degeneration of the thecal layer, and a reduced or absent lumen. To determine spawning frequency, the methods of Fitzhugh et al. (1993) were used to calculate overall counts of active, nonspawning females (i.e., those with vitellogenic oocytes) and spawning females (i.e., those with stage-2 and stage-3 POCs) within each month and during the peak spawning season. The proportion of spawning females was calculated for each month of the spawning season as the number of spawning females divided by the total number of active, nonspawning females plus spawning females. The proportion of spawning females in the peak spawning season was then multiplied by the number of days in the peak spawning season. We assumed that all mature females participated in reproduction throughout the spawning season. A chi-square test was used to determine whether sex ratios significantly differed within and between the 1994–1997 and 2009–2012 sampling periods. Generalized linear models fitted to logistic curves were used to estimate the length at 50% maturity separately for males and females.

RESULTS

Fish Collection

During 1991–2012, Gray Triggerfish sampling ranged from 34.60°N, 76.19°W to 27.23°N, 80.05°W. Overall, 7,685 Gray Triggerfish were collected (44% were male, 54% were female, 2% were of unknown sex; Table 2) from depths of 14–92 m. The mean size of males (337 mm FL) was significantly larger than that of females (304 mm FL; $t = -13.46$, $P < 0.0001$), and the size frequency analysis also indicated a significant difference between the sexes (K–S test: $Z = 6.3$, $P < 0.001$; Figure 2).

Mean size of Gray Triggerfish increased significantly from 1994–1997 to 2009–2012 (two-factor ANOVA, sex: $F_{1,\ 1{,}605} = 95.8$, $P < 0.001$; sampling period: $F_{1,\ 1{,}605} = 109.8$, $P < 0.001$; Table 2), and there was no significant

TABLE 1. Histological criteria (modified from Harris and McGovern 1997 and Moore 2001) that were used to evaluate reproductive phase in Gray Triggerfish. Terminology in the table has been modified according to Brown-Peterson et al. (2011). Photographic examples of each phase are provided in Supplementary Figures S.2 and S.3.

Reproductive phase	Males	Females
Immature (never spawned)	Small transverse section compared with regenerating males; little or no spermatocyte development.	Primary growth oocytes only; no evidence of atresia. In comparison with regenerating females, largest primary growth oocytes are smaller than 60 μm; area of the transverse section of ovary is smaller; lamellae lack muscle and connective tissue bundles and are not as elongate; germinal epithelium along the margin of lamellae is thicker; and ovarian wall is thinner. Oogonia are abundant along the margin of lamellae.
Developing	Limited spermatogenesis in the testes; elongation of lobules and some development of spermatozoa in the testes, but no accumulation in lobules, efferent ducts, and spermatic ducts.	Early: previtellogenic, with only primary growth and cortical alveolar oocytes. Cortical alveolar oocytes are 140–200 μm in diameter. Middle to late: Vitellogenic, most advanced oocytes in the yolk granule or yolk globule stage. Oocytes are 170–400 μm in diameter.
Spawning capable	Early: Spermatozoa are evident in ducts; spermatogenesis amount in the testes ranges from limited to extensive. Greater area of structural tissue in ducts compared to sinuses. Middle (storage): Spermatozoa storage within expanding ducts; over 50% of the sinus area is densely packed with spermatozoa; amount of spermatogenesis in the testes ranges from limited to extensive. Late (recent spawn): large expanded ducts, not as densely packed with spermatozoa. Area of sinuses greater than structural tissue. Empty lobules are usually present toward the center of the testes.	Oocyte maturation in the most advanced oocytes: zona radiata becomes thin, and oocytes are undergoing coalescence of yolk globules, germinal vesicle migration, germinal vesicle breakdown, hydration, or ovulation. Postovulatory follicle complexes are sometimes present. Atresia of vitellogenic and/or hydrated oocytes may be present.
Regressing	Limited spermatogenesis in the testes; some residual spermatozoa in shrunken ducts/lobules and sinuses. Overall number of ducts containing spermatozoa is low. Increase in connective tissue in the testes, proliferating from the center.	More than 50% of vitellogenic oocytes with alpha- or beta-stage atresia.
Regenerating	Little or no spermatocyte development; empty ducts/lobules and sinuses. Large transverse section in comparison with immature males.	Primary growth oocytes only; traces of atresia. In comparison with immature females, largest primary growth oocytes are greater than 60 μm; area of the transverse section of ovary is larger; lamellae have muscle and connective tissue bundles; lamellae are more elongate and convoluted; epithelium along the margin of lamellae is thinner; and the ovarian wall is thicker.
Mature specimen, phase unknown	Mature; but an inadequate quantity of tissue or postmortem histolysis prevents further assessment of reproductive phase.	Mature; but an inadequate quantity of tissue or postmortem histolysis prevents further assessment of reproductive phase.

TABLE 2. Overview of geographic, depth (m), size (FL, mm), and age (years) ranges for male and female Gray Triggerfish over time; and the total number of fish sampled and percentages of males, females, and unknown-sex individuals in samples over time.

Variable	1991–2012	1994–1997	2009–2012
Geographic range	27.23°N, 80.05°W to 34.60°N, 76.19°W	28.95°N, 80.18°W to 34.59°N, 76.95°W	27.23°N, 80.05°W to 34.59°N, 76.93°W
Depth range (m)	14–92	15–92	15–87
Total number of fish sampled	7,685	2,647	1,372
Percent male	43	45	41
Percent female	54	53	56
Percent unknown sex	3	2	3
Overall FL range (mean FL)	82–578 (321)	82–578 (314)	155–523 (346)
Male FL range (mean)	136–578 (337)	137–578 (328)	183–523 (367)
Female FL range (mean)	82–560 (304)	82–474 (296)	155–502 (326)
Overall age range (mean age)	0–13 (5)	0–11 (4)	0–10 (4)
Male age range (mean)	0–13 (5)	0–11 (4)	0–10 (4)
Female age range (mean)	0–13 (5)	0–10 (4)	0–10 (3)

interaction effect ($P = 0.403$). Size frequencies of males and females were significantly different between the two periods (K–S test, males: $Z = 3.8$, $P < 0.001$; females: $Z = 3.8$, $P < 0.001$), with a shift to a greater proportion of larger fish for both sexes in 2009–2012 (Figure 3).

Male size was significantly larger with increasing depth for fish caught in the North Carolina area ($R^2 = 0.49$, $t = 10.3$, $P < 0.001$; Figure 4) and in the South Carolina area ($R^2 = 0.24$; $t = 9.1$, $P < 0.01$). Female size was also significantly larger with depth (North Carolina area: $R^2 = 0.52$, $t = 10.2$, $P < 0.001$; South Carolina area: $R^2 = 0.34$, $t = 12.3$, $P < 0.001$; Figure 4). Additionally, the size frequency of females in both areas indicated that the proportion of larger females was significantly higher in the deeper (40–65-m) zone (K–S test, North Carolina area: $Z = 3.8$, $P < 0.01$; South Carolina area: $Z = 5.6$, $P < 0.01$; Figure 5). Males exhibited a similar trend (North Carolina area: $Z = 4.1$, $P < 0.01$; South Carolina area: $Z = 4.0$, $P < 0.01$; Figure 6).

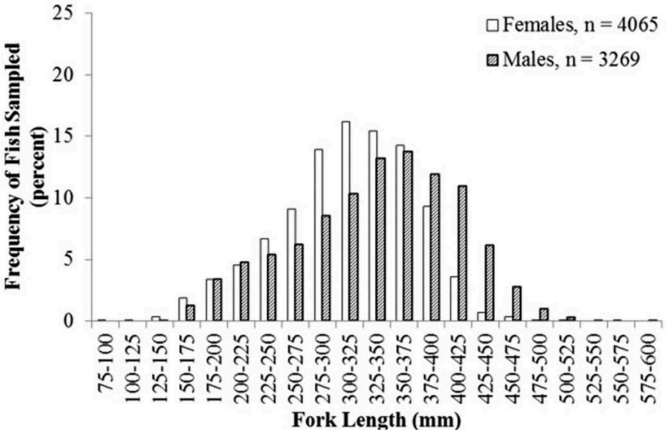

FIGURE 2. Size frequency distributions (FL, mm) for male and female Gray Triggerfish sampled off the southeastern U.S. Atlantic coast from 1991 to 2012 (n = number of specimens).

Age and Growth

During 1994–1997, we collected 2,646 Gray Triggerfish, and age estimates were obtained from 2,484 fish (94% of samples). Among the 1,372 Gray Triggerfish that were caught during 2009–2012, ages were determined for 1,261 fish (92% of samples). The remaining specimens were unused for age estimation because their spines were missing, broken, or unreadable. Exact agreement between readers occurred for 43% of the spine sections, and age estimates agreed within ±1 year for an additional 32% of the sections. The APE in our study was 12%. By comparison, Burton et al. (2015) reported exact between-reader agreement on 34% of age estimates, agreement within ±1 year for 33% of estimates, and an overall APE of 11%. Fioramonti (2012) also reported an APE of 11%.

For fish caught during 2009–2012, the percentage of spines with translucent edges was approximately 50% from April to August and then dropped to less than 30% during September and October (Figure 7). Age frequency distributions were not significantly different between males and females (K–S test: $Z = 0.8$, $P = 0.575$; Figure 8). However, mean ages differed significantly between sexes ($t = -1.97$, $P = 0.02$; Table 2).

A significant difference between the von Bertalanffy growth models for males and females was detected (analysis of RSS: $F_{3,\ 1,258} = 511.62$, $P < 0.0001$; Table 3). Sex-specific growth curves were fitted, yielding the following von Bertalanffy equations (Figure 9; parameters summarized in Table 3): $\text{FL}_t = 419[1 - e^{-0.54(t\ +\ 0.61)}]$ for males and $\text{FL}_t = 352[1 - e^{-0.94(t\ +\ 0.22)}]$ for females.

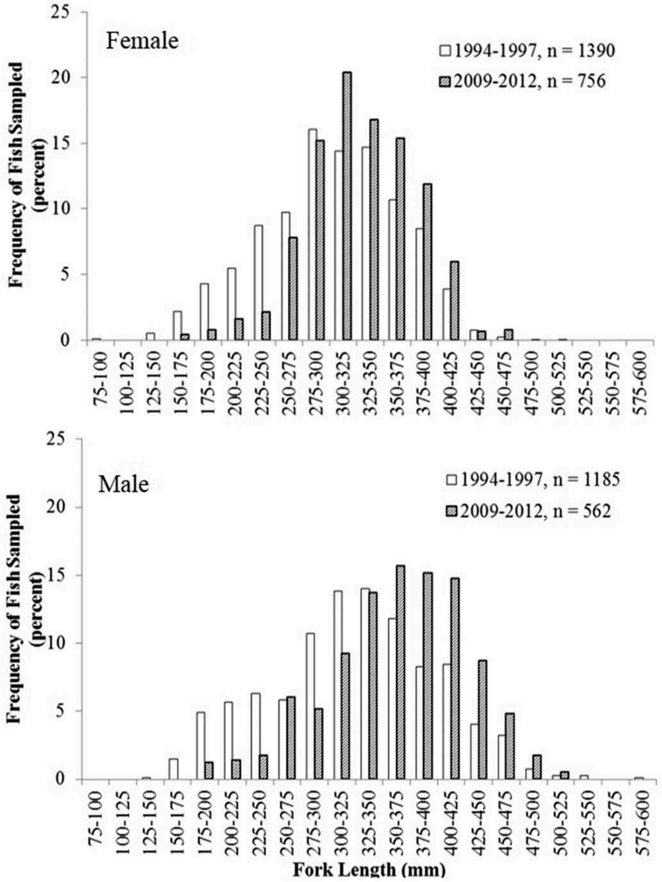

FIGURE 3. Size frequency distributions (FL, mm) of female (upper panel) and male (lower panel) Gray Triggerfish sampled off the southeastern U.S. Atlantic coast during two periods (1994–1997 and 2009–2012; *n* = number of specimens used in the analysis).

Reproduction

Gonads were collected from a total of 7,644 Gray Triggerfish during 1991–2012; sex and reproductive phase were assigned to 6,894 fish (90% of samples). To determine the spawning season, we examined females that were collected throughout all years because the sample sizes of females with spawning indicators in the two sampling periods of interest were low (95 females in 1994–1997 and 6 females in 2009–2012 compared with 176 females in 1991–2012).

In general, for many fish species, the shape of the gonads in males and females is similar in that they (1) consist of two lobes that are posteriorly attached and (2) release the gametes via an oviduct (female) or a spermatic duct (male). The gonads of female Gray Triggerfish are similar in shape to those of other fish species, containing two lobes that are posteriorly attached and release the eggs via the oviduct (Figure S.1). However, we determined that the gonads of male Gray Triggerfish consist of testes, a spermatic duct, and accessory glands (Figures S.1, S.2) and that the accessory glands are used to store spermatozoa before spawning. Close examination of the testes and accessory glands is needed in order to assign the most accurate reproductive phase to males (Table 1; Figures S.1, S.2).

Based on the entire data set (1991–2012), the beginning of the spawning season was April 30—the earliest date (in any year) on which oocyte maturation or POCs were observed in females. The end of the spawning season was September 29, which was the latest date (in any year) on which late-developing oocytes and POCs were present in females. Note that during 1991–2012, only one spawning female was captured in April (out of a total of 71 adult fish sampled), only three were captured in September (out of 1,295 adults), and none was captured in October (out of 40 adults). In addition, no spawning females were captured after August 28 for that month (out of 146 adults). Therefore, a more conservative spawning period estimate of May 5–August 28 was used, resulting in a spawning season of 115 d (Figure 10).

Among females with vitellogenic oocytes, the proportion of females with a spawning indicator (i.e., stage-2 or stage-3 POCs) ranged from 0.03 in May to 0.20 in April (Table 4). The overall proportion of spawning females was 0.095 during the peak spawning season (May–August), so spawning periodicity was approximately every 10 d (or 1/0.095, the reciprocal of the overall proportion of spawning females expressed in days). With a spawning season of approximately 115 d in the U.S. South Atlantic (May 5–August 28), a female can potentially spawn approximately 12 times throughout a given spawning season.

For the remaining analyses, both time periods were used to determine whether any shifts occurred in the sex ratios by FL or the length at 50% maturity. Overall, 4,000 gonad samples were collected during the two sampling periods (2,633 samples in 1994–1997; 1,367 samples in 2009–2012). Sex and reproductive phase were assigned to 3,700 fish (93% of the samples). The overall male : female sex ratio for Gray Triggerfish collected during 1994–1997 was 1:1.19 and differed significantly from a 1:1 ratio (Table 5). Females were more abundant than males in size-classes ≤ 350 mm FL, and the sex ratio differed significantly from 1:1 for 151–350-mm FL fish. Males larger than 401 mm FL were more abundant than females, and the sex ratio significantly differed from 1:1 for 401–500-mm FL fish. Sample sizes in size-classes greater than 500 mm FL were low (i.e., <10 fish); therefore, chi-square analyses were not performed.

The overall male : female sex ratio for Gray Triggerfish collected during 2009–2012 was 1:1.34 and differed significantly from a 1:1 ratio (Table 5). Females 350 mm FL or smaller were more abundant than males of those sizes, and the sex ratio significantly differed from 1:1 for 201–350-mm FL fish. However, males were more abundant in the smallest size-class (151–200 mm FL), and the sex ratio did not significantly differ from 1:1. Males that were larger than 400 mm FL were more abundant than females, and the sex ratio differed

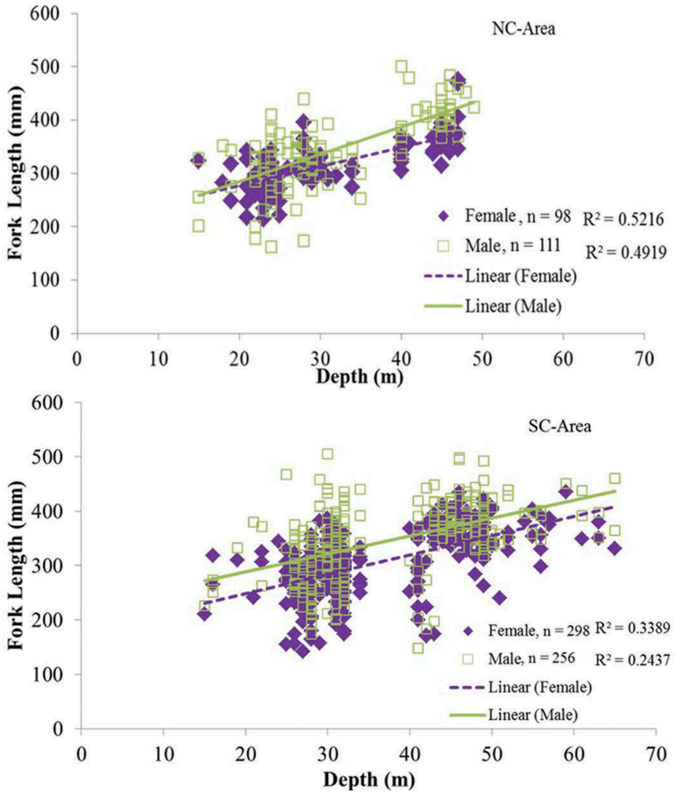

FIGURE 4. Sizes (FL, mm) of male and female Gray Triggerfish in relation to depth (m) for fish sampled during 2004–2012 from the North Carolina (NC) area (upper panel) and the South Carolina (SC) area (lower panel; *n* = number of specimens used in analysis). Linear regression analysis of the slopes was used (NC area: R^2 = 0.5216 for females, 0.4919 for males; SC area: R^2 = 0.3389 for females, 0.2437 for males).

significantly from 1:1 for 401–500-mm FL males. We had low sample sizes (i.e., <10 fish) for males and females that were 501–550 mm FL, so a chi-square analysis was not performed for this size-class.

Females were more abundant than males at most ages except ages 7 and 10 (Table 6). The sex ratio significantly differed from 1:1 for ages 2–4 but did not differ for age 1 or ages 5–8. Chi-square analyses for ages 0, 9, and 10 were not performed due to low sample sizes.

For the periods 1994–1997 and 2009–2012, immature Gray Triggerfish made up 3% of the specimens for which reproductive phase was determined (*n* = 114; 91 fish in 1994–1997 and 23 fish in 2009–2012). Correct assignment of reproductive tissue to the "immature" and "regenerating" gonad categories was indicated by (1) the complete or near-complete overlap in the left tail of the size frequency distributions for definitely mature (i.e., developing, spawning, and regressing phases) and regenerating-phase specimens and (2) the minimal overlap in the size frequency distributions for immature and regenerating-phase specimens (Figure 11).

For samples collected in 1994–1997, the smallest mature male was 165 mm FL, and the largest immature male was 265 mm FL. The youngest mature male was age 0, and the oldest immature male was 4 years. Male size at 50% maturity was 184 mm FL (95% confidence interval [CI] = 175–191 mm), and all males larger than 271–280 mm FL were mature. The smallest mature female was 152 mm FL, and the largest immature female was 297 mm FL. The oldest immature female was 3 years. Female size at 50% maturity was 177 mm FL (95% CI = 167–184 mm), and all females larger than 251–260 mm FL were mature, with the exception of the largest immature female recorded at 297 mm FL, which was 54 mm larger than the next-largest immature female at 243 mm FL. Among age-1 fish, 79% of males and 90% of females were sexually mature.

For 2009–2012 samples, the smallest mature male was 183 mm FL, and the youngest mature male was age 0; the largest immature male was 268 mm FL, and the oldest immature male was 2 years. Male size at 50% maturity was 174 mm FL (95% CI = 95–205 mm); all males larger than 281–290 mm FL and older than age 2 were mature. The smallest mature female was 179 mm FL, and the youngest mature female was age 0; the largest immature female was 290 mm FL, and the oldest immature female was age 4. Female size at 50% maturity was 190 mm FL (95% CI = 166–210 mm), and all females were mature by 301–310 mm FL. Among age-1 fish, 92% of males and 87% of females were sexually mature.

DISCUSSION

Results from the present study provide key life history information for an exploited population of Gray Triggerfish. This study is the first to comprehensively describe age, growth, and reproduction for a *Balistes* species. We documented that the Gray Triggerfish is a sexually dimorphic species, with adult males attaining a larger size at age and a larger maximum size than females. The species is characterized by a medium size at maturity and a relatively early age at maturity. We also found that some shifts in population attributes have coincided with a period of apparent increase in fishing pressure.

Population Size Structure, Age, and Growth

The mean length of males was significantly larger than that of females. Similar findings have been reported for Gray Triggerfish in the Gulf of Mexico (Hood and Johnson 1997; Ingram 2001). Males and females also exhibited different growth rates in our study, with males attaining a larger size at age and a greater asymptotic length. Ingram (2001) documented a similar trend with fish collected from Alabama. To some degree, this may be related to the mating and nesting behaviors documented for this species. Simmons and Szedlmayer (2012) studied the reproductive behavior of Gray Triggerfish utilizing artificial reef habitats in the northern Gulf

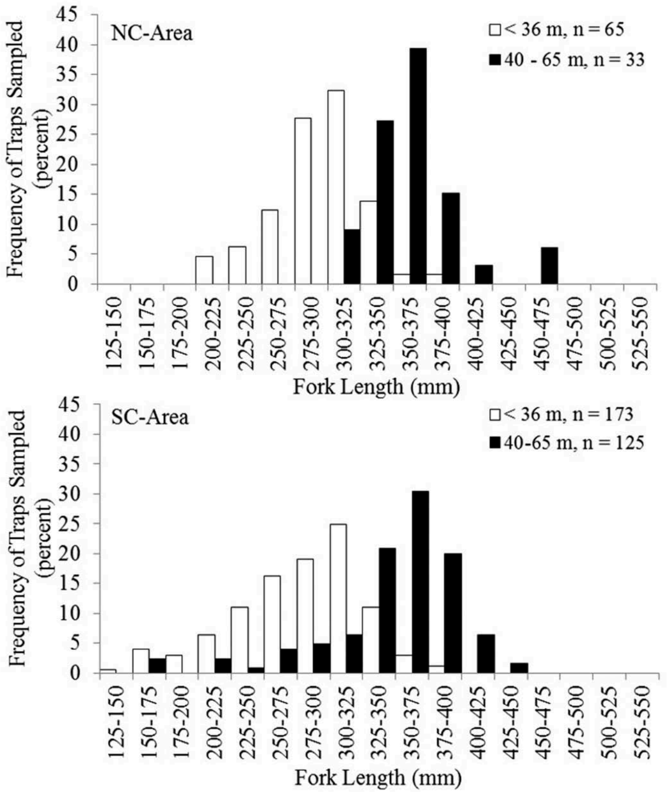

FIGURE 5. Size-class frequency distributions (FL, mm) of female Gray Triggerfish sampled from two depth ranges (open bars = <36 m; black bars = 40–65 m) in the North Carolina (NC) area (upper panel) and the South Carolina (SC) area (lower panel) during 2004–2012 (*n* = number of specimens used in analysis).

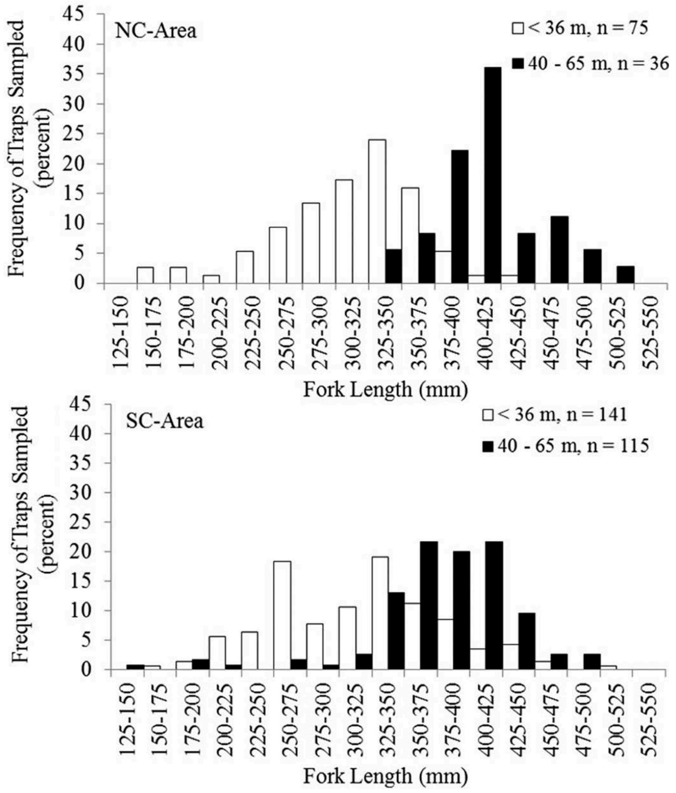

FIGURE 6. Size-class frequency distributions (FL, mm) of male Gray Triggerfish sampled from two depth ranges (open bars = <36 m; black bars = 40–65 m) in the North Carolina (NC) area (upper panel) and the South Carolina (SC) area (lower panel) during 2004–2012 (*n* = number of specimens used in analysis).

of Mexico; they reported that a large dominant male patrols a nesting territory, builds and maintains multiple nests within the territory, and continues to guard the nesting area after fertilization. The larger size of males is advantageous given that they need to defend nests in order to optimize the survival of the eggs. The relatively small females also exhibit parental investment behaviors. Prior to spawning, the females inspect potential nests. Once a female deposits eggs into a nest, she

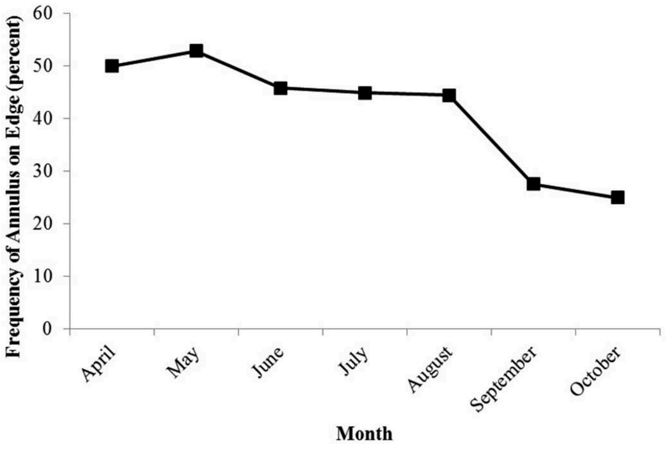

FIGURE 7 Percent frequency of annulus (i.e., the translucent zone) presence on the edge of the first dorsal spine in Gray Triggerfish collected off the southeastern U.S. Atlantic coast during each month.

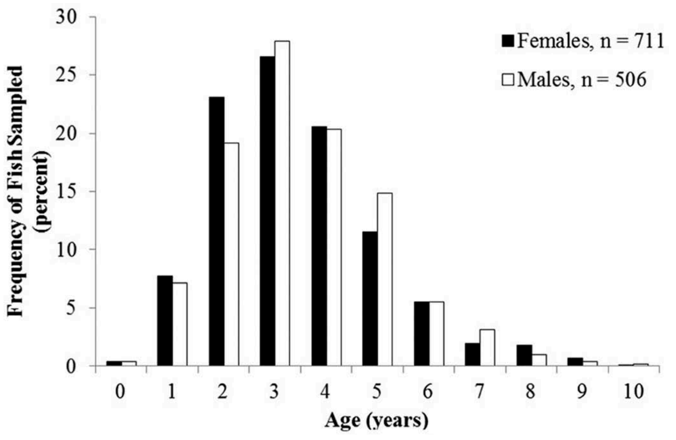

FIGURE 8. Age frequency distributions of female and male Gray Triggerfish sampled off the southeastern U.S. Atlantic coast during 2009–2012 (*n* = number of specimens).

TABLE 3. Parameters (L_∞ = asymptotic length [FL, mm]; k = Brody growth coefficient; t_0 = theoretical age [years] at zero length) derived from von Bertalanffy growth equations that were fitted to observed size-at-age data for Gray Triggerfish sampled off the southeastern U.S. Atlantic coast. Growth curves were calculated for (1) each sex; (2) the combined data set, including juveniles caught from *Sargassum* habitat; and (3) the combined data set, excluding juveniles from *Sargassum*.

Sex	n	L_∞ (SE)	k (SE)	t_0
Male	549	419 (1.3)	0.54 (0.010)	–0.61
Female	709	352 (0.7)	0.95 (0.001)	–0.22
Combined	1,258	382 (0.7)	0.67 (0.008)	–0.47
Combined (excluding juveniles)	1,247	419 (2.3)	0.30 (0.009)	–2.39

guards the eggs in addition to tending to them by fanning and blowing on the eggs to provide oxygenation. Females appear to stay within 1 m of their eggs until they hatch, which can take up to 48 h (Simmons and Szedlmayer 2012).

The mean size of males and females increased during the same period that fishing pressure appeared to increase across the region; many studies have reported that fish stocks experiencing overfishing usually exhibit the opposite trend. The Speckled Hind *Epinephelus drummondhayi* in southeastern U.S. Atlantic waters is considered an overfished species, and Ziskin et al. (2011) documented a decrease in the average size of Speckled Hind caught during 2004–2007 relative to historical data collected in 1979–1981. Similarly, a comparison of recent data to historical data revealed a decrease in the size of Scamp *Mycteroperca phenax* in U.S. South Atlantic waters (Harris et al. 2002). A decline in mean sizes after 15 years of intense fishing pressure was also reported for several porgy and snapper species in waters off North Carolina (Parker and Mays 1998).

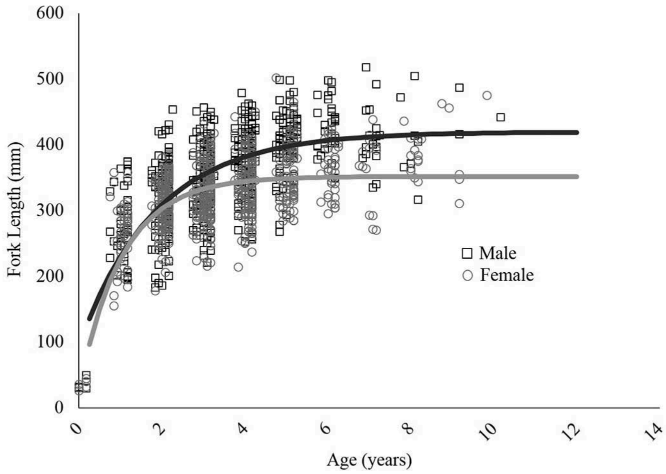

FIGURE 9. Fork length at age for male and female Gray Triggerfish collected off the southeastern U.S. Atlantic coast during 2009–2012, with von Bertalanffy growth curves fitted to the sex-specific data sets (black line = growth curve for males; gray line = growth curve for females). See Table 3 for a summary of the von Bertalanffy parameters.

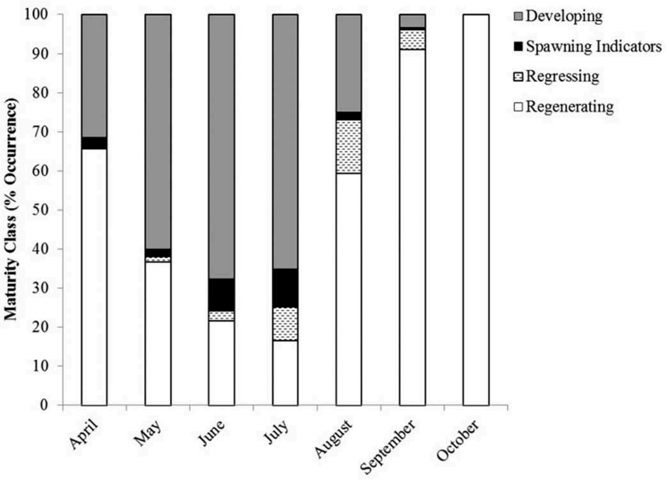

FIGURE 10. Reproductive seasonality of female Gray Triggerfish collected off the southeastern U.S. Atlantic coast during 1991–2012. See Methods for a description of the spawning indicators.

The increase in mean sizes and the greater proportion of larger individuals within the Gray Triggerfish population may partially be explained by a corresponding decline in the abundances of co-occurring reef fish species that potentially compete with the Gray Triggerfish for resources (Ballenger et al. 2013). Adult Gray Triggerfish are generalists in their feeding habits (Blitch 2000; Goldman et al. 2016). They consume a wide range of invertebrate prey, including sponges, crustaceans (e.g., barnacles and crabs), echinoderms (e.g., sea urchins, sand dollars, and sea stars), and mollusks (e.g., bivalves, gastropods, and cephalopods). They have also been observed to feed on fishes (V.S., unpublished data). Many of the declining reef fish species exhibit more specialized feeding strategies and have narrower diets (Tremain and Adams 2012). Thus, declines in co-occurring species, such as the Scamp, Red Porgy *Pagrus pagrus*, and Speckled Hind, may have contributed to an increase in the availability of food items for Gray Triggerfish, which in turn could have led to increased growth rates and ultimately a shift in the proportion of larger individuals within the Gray Triggerfish population. Further research is needed to examine this anomaly.

The results from our examination of spine margin zones indicated that annulus formation occurred in the late spring to early summer, which is consistent with the findings of other studies (Moore 2001; Burton et al. 2015). The formation of the translucent zone (as seen under transmitted light) during summer months would be expected given that translucent zones represent periods of slower somatic growth. Gray Triggerfish generally spawn during summer (May–August) and therefore are investing more energy into reproduction to optimize the

TABLE 4. Spawning frequency of female Gray Triggerfish based on histological data from samples collected in 1991–2012. Spawners had middle or late postovulatory follicle complexes (POCs). Active nonspawners were reproductively active (i.e., vitellogenic oocytes were present) but did not have stage-2 or stage-3 POCs.

Month	Number of active nonspawners	Number of spawners	Proportion spawners
Apr	4	1	0.20
May	129	4	0.03
Jun	412	42	0.09
Jul	541	71	0.12
Aug	155	13	0.08
Sep	15	3	0.17
May–Aug	1,237	130	0.01

TABLE 5. Sex ratio within each size-class (FL, mm) for Gray Triggerfish collected off the southeastern U.S. Atlantic coast during 1994–1997 and 2009–2012.

FL (mm)	Total number of fish	Male : female ratio	*P*
	1994–1997		
151–200	105	1:1.76	<0.05
201–250	327	1:1.42	<0.05
251–300	557	1:1.86	<0.001
301–350	737	1:1.21	<0.05
351–400	500	1:1.08	0.37
401–450	204	1:0.44	<0.001
451–500	48	1:0.07	<0.001
501–550	6		
551–600	1		
	2009–2012		
151–200	11	1:0.38	0.13
201–250	39	1:2.00	0.04
251–300	236	1:2.69	<0.001
301–350	417	1:2.16	<0.001
351–400	369	1:1.17	0.13
401–450	180	1:0.36	<0.001
451–500	39	1:0.18	<0.001
501–550	4	1:0.33	

TABLE 6. Sex ratio by age for Gray Triggerfish collected off the southeastern U.S. Atlantic coast during 2009–2012.

Age (years)	Total number of fish	Male : female ratio	*P*
0	2	1:1.00	
1	82	1:1.41	0.12
2	257	1:1.73	<0.001
3	327	1:1.32	<0.05
4	248	1:1.41	<0.05
5	157	1:1.09	0.58
6	67	1:1.39	0.18
7	30	1:0.88	0.72
8	18	1:2.60	0.06
9	7	1:2.50	
10	2	1:1.00	

survival of their offspring while investing less energy in somatic growth. Moore (2001) concluded that increment formation in Gray Triggerfish of the U.S. South Atlantic occurred in June, and Burton et al. (2015) reported that increment formation took place in June and July. Johnson and Saloman (1984) reported that increment formation in Gray Triggerfish occurred from April to August in the Gulf of Mexico. Other reef fishes also exhibit spring or summer increment formation. For example, Snowy Grouper *Hyporthodus niveatus* in North Carolina and South Carolina offshore waters form annuli during April and May (Wyanski et al. 2000). For Yellowtail Snapper *Ocyurus chrysurus* in Florida, annulus formation occurs during March and April (Garcia et al. 2003). Speckled Hind in Atlantic waters form annuli from June to August (Ziskin et al. 2011).

The first dorsal spine has been the main aging structure used for triggerfish species for over 30 years (Ofori-Danson 1989; Ingram 2001; Moore 2001; Bernardes 2002; Aggrey-Fynn 2009; Burton et al. 2015). This external bony structure is used in defense and often breaks and twists during a fish's lifetime (Kelly 2014). Studies of other species have demonstrated that external structures, including spines, significantly underestimate the true age of fish (Buckmeier et al. 2012; Gu et al. 2013; Lozano et al. 2014). Additionally, in comparison with sagittal otolith-based age estimates, dorsal spines were found to underestimate the age of Gray Triggerfish (Shervette and Dean 2015). Ages based on dorsal spines have yet to be directly validated (i.e., confirming the periodicity of growth zone formation), and other studies have reported difficulties in using this structure for estimating Gray Triggerfish ages (Fioramonti 2012; Burton et al. 2015). For example, Burton et al. (2015) reported relatively low agreement in ages produced by two readers: perfect agreement occurred for 34% of their samples (in our study, exact agreement = 43%), and overall agreement increased to 67% when including estimates that agreed within ±1 year (in our study, overall agreement including estimates within ±1 year = 75%). Fioramonti (2012) encountered similar issues with reader agreement, reporting an APE of 11% (in our study, overall APE = 12%).

Two studies have attempted to validate ages for dorsal spines by using oxytetracycline to chemically mark laboratory-held Gray Triggerfish collected from the Gulf of Mexico

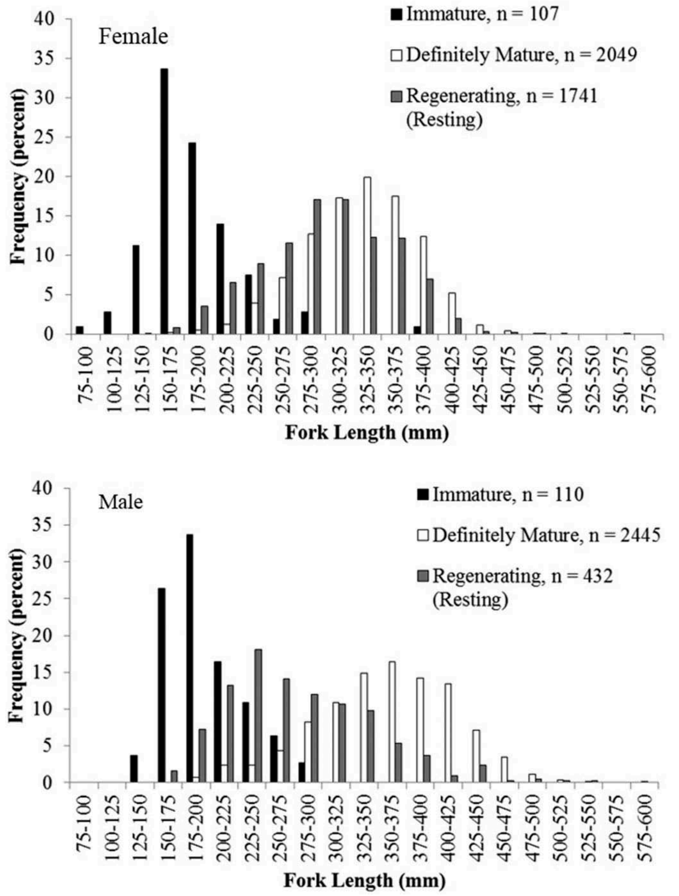

FIGURE 11. Size frequency distributions (FL, mm) of female (upper panel) and male (lower panel) Gray Triggerfish with gonads categorized as immature, definitely mature (i.e., developing, spawning capable, or regressing), or regenerating. Fish were sampled off the southeastern U.S. Atlantic coast during 1991–2012.

(Hood and Johnson 1997; Fioramonti 2012). Hood and Johnson (1997) marked 12 Gray Triggerfish and held them for 1 year before sacrificing the fish and processing them for age determination. In all 12 fish, the chemical mark was still on the edge of the spine, indicating that no additional growth had occurred on the spine during the year in captivity. In contrast, Fioramonti (2012) marked four adult Gray Triggerfish and held them for 8 months, after which they were sacrificed and processed for age determination. Fioramonti (2012) reported that one translucent zone formed on the spines beyond the chemical mark. Due to the conflicting results of these two studies, spines have yet to be truly validated as an accurate aging structure for this species.

The first dorsal spine was used in our study because it is currently the accepted aging structure for Gray Triggerfish. However, whether our age data represent the true age is still unknown, so caution must be used when interpreting these data and making comparisons with other studies that have used dorsal spines to estimate age.

In the present study, male and female Gray Triggerfish sampled in 2009–2012 ranged in age from 0 to 10 years. Only one other study has reported age estimates for Gray Triggerfish from approximately the same period. Fioramonti (2012) reported similar maximum ages for males (8 years) and females (9 years) collected in 2003–2010; however, they also noted the capture of a 14-year-old fish of unknown sex. A few studies that have combined age data across several decades or that have presented data from earlier periods have observed older Gray Triggerfish (Johnson and Saloman 1984; Fioramonti 2012; Burton et al. 2015). Johnson and Saloman (1984) reported maximum ages of 13 years for males and 12 years for females, but their study period was 1979–1982. Burton et al. (2015) reported a maximum age of 15 years. Differences in maximum age between our study and previous studies may not be biologically significant—rather, they may be related to the difficulty or inaccuracy of using dorsal spines to estimate the age of Gray Triggerfish. In addition, other studies have focused on fishery-dependent samples, have utilized samples from earlier periods, or both.

Several studies have reported that Gray Triggerfish exhibit moderately rapid growth and obtain a relatively large size by the end of their first year (Table 7), a conclusion that is generally supported by our results. In fact, when we included juvenile Gray Triggerfish sampled from *Sargassum* habitat, the growth rates we calculated for males and females were among the highest reported (Table 7). However, care should be taken when comparing von Bertalanffy parameter values among studies. Some studies have utilized specialized rules for adjusting increment counts to age estimates (Ingram 2001; Fioramonti 2012; Burton et al. 2015), while other studies have used back-calculated sizes in the growth model (Johnson and Saloman 1984; Escorriola 1991; Bernardes 2002) or have forced t_0 to equal zero (Ofori-Danson 1989). Several studies have combined data from females and males into one growth model (Ofori-Danson 1989; Escorriola 1991; Burton et al. 2015). Only one other study has used juveniles sampled from *Sargassum* in estimating the growth of Gray Triggerfish (Fioramonti 2012). Regional variation in growth rates within a species is not unusual (Brander 1994), so some differences in growth for Gray Triggerfish can be partly explained by regional differences (Ofori-Danson 1989; Bernardes 2002; Aggrey-Fynn 2009; Kacem et al. 2015). Several studies have reported that growth parameter estimates differ depending on the sample sources (Ingram 2001; Fioramonti 2012). Our study is the only published work based exclusively on fishery-independent samples (Table 7), thereby reducing size- or gear-related biases that might occur with fishery-dependent sources but also hindering the direct comparison of our growth rate estimates with those of other studies.

The youngest age-class (age 0) was observed infrequently for both sexes in the current study. The low sample sizes of age-0 Gray Triggerfish could reflect the association of early life stages with *Sargassum* and thus their lack of availability to the bottom gears used. The exact age at which larval and juvenile Gray Triggerfish cease to associate with *Sargassum* and become established in reef habitats is unknown. Another possible factor influencing the low sample sizes of smaller and younger specimens in this study is the abundance of predators in the chevron traps. Smaller fish may exhibit predator avoidance if larger predators are inside the traps.

Reproduction

The Gray Triggerfish is a gonochoristic species, and females are group-synchronous, indeterminate batch spawners (Figure S.3). We found that Gray Triggerfish in U.S. South Atlantic waters spawned from April to September, with peak spawning in May–August, which overlaps with the spawning season reported for this species in the Gulf of Mexico (Hood and Johnson 1997; Ingram 2001; Lang and Fitzhugh 2015). Gray Triggerfish from the U.S. South Atlantic appear to have a longer spawning season (conservative estimate was 115 d based on the occurrence of actively spawning females) than those in the northern Gulf of Mexico, where spawning occurs over an 86-d period starting in May (Lang and Fitzhugh 2015). Gray Triggerfish in the Tunisian fishery spawn during July–September (Kacem and Neifar 2014); those inhabiting coastal waters of Ghana spawn in October–December (Ofori-Danson 1990); and those in Brazilian waters spawn during November–January (Bernardes and Dias 2000). A combination of several factors may explain the differences in the timing and length of spawning season among studies. First, regional variation in factors such as temperature, fish community composition, fishing pressure, and habitat complexity could play a role in regulating the reproductive season. Second, the method used to estimate reproductive season varied among studies; our study and two other studies based reproductive seasonality on the histological examination of gonads (Bernardes and Dias 2000; Lang and Fitzhugh 2015), whereas the other studies relied on changes in gonadal weight or on macroscopic assessment of gonad phases. Third, differences in sample sources (fishery dependent versus fishery independent) could have impacted the findings. Lastly, sampling intensity, duration, and total sample numbers varied among the studies; we report data from examining over 6,500 gonad samples, whereas another study examined only 658 samples (Ofori-Danson 1990).

We estimated that females could spawn up to 12 times throughout the spawning season, which is similar to the 8–11 times estimated for Gray Triggerfish in the Gulf of Mexico (Lang and Fitzhugh 2015). The Gray Triggerfish exhibits a relatively unique reproductive strategy compared with other large-bodied species targeted by fisheries in southeastern U.S. Atlantic waters and in the Gulf of Mexico (Johannes 1978; Lambert and Ware 1984; Murua and Saborido-Rey 2003). The combined benefits of major parental investments in establishing reproductive territories, benthic nesting and guarding by both adults (Simmons and Szedlmayer 2012), relatively high fecundity that increases with size (Lang and Fitzhugh 2015), a spawning season that extends for several months, and up to 12 spawns within a season may result in a higher survival rate for larval Gray Triggerfish in comparison with the larvae of broadcast-spawning species. Research on larval survival rates would be necessary to verify this.

The gonads of male Gray Triggerfish are unique in their structure and function in that they consist of testes, a spermatic duct, and accessory glands. The accessory glands are used to store spermatozoa before spawning (Figure S.1); the purpose of storing spermatozoa in the accessory glands could be related to differences in the reproductive behavior of Gray Triggerfish compared with other reef fish species. Male Gray Triggerfish have been observed to build several nests in the substrate, and females will lay their eggs in those nests (Simmons and Szedlmayer 2012). Considering the number of nests constructed and the distance between each nest, the storage of spermatozoa in the male accessory glands would be necessary to ensure fertilization of the eggs in each nest.

In summary, the present results provide insights into the Gray Triggerfish population off the southeastern U.S. Atlantic coast and constitute essential information for fisheries management. Considering that males and females have significantly different von Bertalanffy growth parameters, the sexes may need to be modeled separately in stock assessments. Additionally, as fishers tend to remove larger fish from the population, males may be removed more frequently than females. Furthermore, as the populations of other reef fish species decline, Gray Triggerfish may be experiencing an increase in the availability of prey and other resources, leading to the observed increase in growth rates and the upward shift in the proportion of larger individuals within the population.

Due to tighter regulations on snapper and grouper fisheries, the Gray Triggerfish has become a more targeted and economically valuable species in southeastern U.S. waters of the Atlantic. We did not detect the typical life history shifts that have been observed to correspond with increases in fishing pressure (Harris and McGovern 1997; Wyanski et al. 2000; Ziskin et al. 2011; Hunter et al. 2015), but this does not mean that Gray Triggerfish are not experiencing negative impacts. The species' relatively unique reproductive strategy among the fishes in its management group may make it necessary to expand our current understanding of the life history indicators of overfishing, as such indicators are mainly based on data from broadcast-spawning species that produce pelagic larvae. Fisheries biologists and managers should continue to evaluate potential impacts on the Gray Triggerfish and establish management regulations that consider the region-specific reproductive season, size and age at maturity, and sex-specific growth documented in this study.

TABLE 7. Comparison of von Bertalanffy growth parameter estimates (L_∞ = asymptotic length [FL, mm]; k = Brody growth coefficient; t_0 = theoretical age [years] at zero length) for Gray Triggerfish, as calculated in the present study and in previous studies (FL = Florida; NC = North Carolina; AL = Alabama; GOM = Gulf of Mexico; NA = not available or not examined).

Study	Source	L_∞ (mm FL)	k	t_0	Peak increment formation; spawning season	Notes
Present study	Fishery-independent data, FL–NC (2009–2012)	Females: 352 Males: 419 All: 382 All except juveniles: 419	Females: 0.95 Males: 0.54 All: 0.67 All except juveniles: 0.30	Females: –0.22 Males: –0.61 All: –0.47 All except juveniles: –2.39	Apr–Jun; Apr–Sep	Significant difference between growth curves for females and males
Burton et al. 2015	Commercial/recreational fisheries, FL–NC (1990–2012)	All: 466	All: 0.38	All: –1.58	Jun–Jul; NA	Adjusted ages based on margin
Kacem and Neifar 2014; Kacem et al. 2015	Commercial samples from Tunisia (2008–2010)	Females: 417 Males: 420 All: 417	Females: 0.24 Males: 0.23 All: 0.24	Females: –0.07 Males: –0.12 All: –0.10	Feb; Jul–Sep	Spawning season based on gonadosomatic index
Fioramonti 2012	Fishery-independent data and commercial/recreational fisheries, northern GOM (2003–2010)	Females: 381 Males: 403 All: 521	Females: 0.50 Males: 0.49 All: 0.27	Females: –0.02 Males: –0.01 All: –0.12	Dec–Jan; NA	Adjusted ages based on difference between birthdate and translucent zone formation; included juveniles collected from *Sargassum* habitat
Bernardes 2002	Commercial samples from Brazil (1984–1985)	Females: 505 Males: 516 All: 510	Females: 0.27 Males: 0.26 All: 0.27	Females: –0.03 Males: –0.01 All: –0.12	Apr–May and Sep–Nov (i.e., two periods); NA	Used back-calculated size-at-age values
Ingram 2001	Recreational fisheries, AL; and GOM groundfish survey (1996–2000)	Females: 514 Males: 598 All: 583	Females: 0.21 Males: 0.20 All: 0.18	Females: –1.61 Males: –1.37 All: –1.58	Dec–Jan; May–Aug	Adjusted age based on a formation date of January 1, a spawning date of July 1, and the date of capture
Hood and Johnson 1997	Commercial/recreational fisheries, northern GOM (1995–1996)	Females: 421 Males: 645 All: 556	Females: 0.33 Males: 0.16 All: 0.15	Females: –1.20 Males: –1.80 All: –1.90	NA; Jun–Sep	Could not determine when increment formed
Escorriola 1991	Commercial/recreational Fisheries, FL–NC (1981–1989)	All: 571	All: 0.19	All: –0.15	Jul–Sep; NA	Used back-calculated size-at-age values
Ofori-Danson 1989	Fishery-independent data, Ghana (1980)	All: 408	All: 0.43	All: 0.00	NA; NA	Forced $t_0 = 0$
Johnson and Saloman 1984	Commercial samples from Panama City, FL (1979–1982)	Females: 438 Males: 492 All: 466	Females: 0.38 Males: 0.38 All: 0.38	Females: 0.15 Males: 0.23 All: 0.19	Jun–Jul; NA	Used back-calculated size-at-age values

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