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Marcus Drymon

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research paper

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Amanda E Jefferson [1]*
Robert J Allman [2]
Ashley E Pacicco [3]
James S Franks [4]
Frank J Hernandez [4]
Mark A Albins [5]
Sean P Powers [5, 6]
Robert L Shipp [5]
J Marcus Drymon [1]

[1] Mississippi State University, Coastal Research and Extension Center, 1815 Popps Ferry Road, Biloxi, Mississippi 39532.

[2] National Marine Fisheries Service, Southeast Fisheries Science Center, Panama City Laboratory, 3500 Delwood Beach Road, Panama City, Florida 32408.

[3] Riverside Technology, Inc., National Marine Fisheries Service, Southeast Fisheries Science Center, Panama City Laboratory, 3500 Delwood Beach Road, Panama City, Florida 32408.

[4] Gulf Coast Research Laboratory, Center for Fisheries Research and Development, University of Southern Mississippi, 703 E Beach Drive, Ocean Springs, Mississippi 39564.

[5] Department of Marine Sciences, University of South Alabama, LSCB-25, Mobile, Alabama 36688.

[6] Dauphin Island Sea Lab, 101 Bienville Boulevard, Dauphin Island, Alabama 36528.

** Corresponding author email: <amanda.jefferson@msstate.edu>.*

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ABSTRACT.—The overexploitation of many traditionally targeted reef fishes, such as red snapper, *Lutjanus campechanus* (Poey, 1860), alongside the implementation of increasingly restrictive management measures on those species, has led to increased targeting of conventionally discarded Gulf of Mexico gray triggerfish, *Balistes capriscus* Gmelin, 1789, commercially and recreationally. The goal of this study was to assess age and growth of gray triggerfish from the Alabama Artificial Reef Zone in the north-central Gulf of Mexico. Gray triggerfish (n = 1135) were collected predominantly from artificial habitat during 1999–2017. Specimens were sexed macroscopically and ages were assigned by counting translucent increments in sections of the first dorsal spine. Fish ranged in size from 22 to 617 mm fork length. The oldest female was assigned an age of 9 yrs; the oldest male, 10 yrs. A suite of growth models was tested to develop combined and sex-specific models. The von Bertalanffy growth function best fit the combined data with parameters L_∞ = 488.63 (SE 5.19), k = 0.57 (SE 0.02), and t_0 = −0.27 (SE 0.03). Mean size-at-age differed between sexes for six of the eight ages which possessed sample sizes large enough to make comparisons. Growth differed between sexes, and the best-fitting version of the von Bertalanffy growth function permitted L_∞ to vary by sex [female L_∞ = 480.26 (SE 7.99); male L_∞ = 532.89 (SE 8.95); k = 0.44 (SE 0.04); t_0 = −0.78 (SE 0.16)]. These findings enhance our knowledge of the age and growth of Gulf of Mexico gray triggerfish.

Gray triggerfish, *Balistes capriscus* Gmelin, 1789, occur in the eastern and western Atlantic Ocean, and occupy waters from Nova Scotia to Argentina, including the Gulf of Mexico (GOM) (Briggs 1958, Moore 1967). Diet studies suggest that gray triggerfish consume a variety of invertebrates, including barnacles, bivalves, echinoderms, and crabs (Vose and Nelson 1994). Gray triggerfish exhibit unique reproductive strategies, including nest building, harem spawning behavior, parental care of eggs, and territoriality (MacKichan and Szedlmayer 2007, Simmons 2008, Simmons and Szedlmayer 2012). In the GOM, peak spawning occurs during June and July (Ingram 2001, Simmons and Szedlmayer 2012, Lang and Fitzhugh 2015). Larval and juvenile gray triggerfish are pelagic and inhabit the holopelagic *Sargassum* community for several months before settling to benthic reefs (Dooley 1972, Wells and Rooker 2004, Simmons and Szedlmayer 2011). Once individuals settle to reefs, they display high site fidelity (Ingram 2001, Addis et al. 2013). In the north-central GOM, natural reefs are scarce, so gray triggerfish commonly reside on artificial reefs such as those present in the >3200 km^2 Alabama Artificial Reef Zone (AARZ) (Fig. 1) (Minton and Heath 1998), a recreational fishing hot spot in the region (Karnauskas et al. 2017).

The reef-building program in the AARZ began in 1953 and is the largest in the United States. Since then, various artificial structures, including wire-frame chicken transport devices, purpose-built concrete pyramids, car bodies, barges, tanks, liberty ships, and planes, have been intentionally placed on the seafloor in the AARZ with the primary goal of enhancing recreational fishing opportunity (Minton and Heath 1998). Szedlmayer and Shipp (1994) estimated that as many as 6000 artificial reefs exist in the AARZ and postulated that the reefs attract fishes and may enhance productivity as well. This is due to the increased vertical relief and complexity afforded by the artificial reefs (Hixon and Beets 1989, Shipp 1999, Strelcheck et al. 2005). Increases in the catch of reef fishes, such as red snapper, *Lutjanus campechanus* (Poey 1860), and gray triggerfish, have been directly attributed to the presence of artificial reefs in the AARZ (Minton and Heath 1998, Shipp and Bortone 2009).

GOM gray triggerfish are managed under the 1984 Reef Fish Fishery Management Plan by the Gulf of Mexico Fishery Management Council (GMFMC) and National Marine Fisheries Service (NMFS) (GMFMC and NMFS 1981). In 2006, a Southeast Data Assessment and Review (SEDAR) benchmark assessment was conducted for GOM gray triggerfish. At the time, the only regulations for the stock were a 12-inch (30.5 cm) minimum total length and inclusion in the recreational reef fish bag limit (20 reef fish per day). The results of this assessment suggested that the GOM gray triggerfish stock was undergoing overfishing, and a rebuilding period of 10 yrs was established (SEDAR-9 2006). An update assessment conducted in 2011 revised the status of GOM gray triggerfish to overfished and experiencing overfishing (SEDAR-9 2011). Consequently, additional management actions were implemented, which included increasing the minimum size limit, reducing catch limits and targets, establishing a species-specific bag limit, and enacting an annual closed season (SEDAR-43 2015).

Concomitant with increasingly stringent regulations, GOM gray triggerfish catch has generally declined since 1991. The GOM gray triggerfish fishery is dominated by recreational landings, with commercial landings comprising only a small fraction of the total harvest [National Marine Fisheries Service Fisheries Statistics Division, pers comm (date of inquiry: 25 January, 2018)]. Commercial harvest peaked in 1999 at 43.9 t, generally exhibited a declining trend through 2010 (5.3 t), and exhibited a slightly increasing trend in recent years from 2011 to 2016 (27.7 t harvested in 2016) [National Marine Fisheries Service Fisheries Statistics Division, pers comm (date of

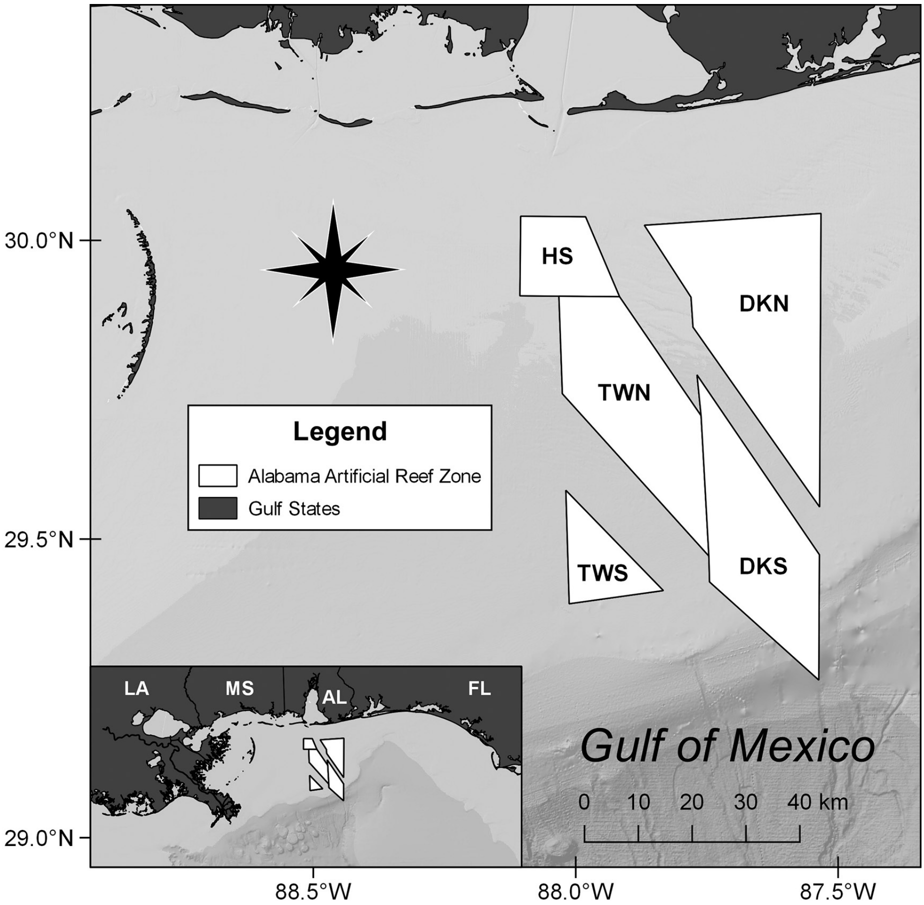

Figure 1. Alabama Artificial Reef Zone map. Abbreviations are as follows: HS: Hugh Swingle General Permit Area; DKN: Don Kelley North General Permit Area; TWN: Tatum Winn North General Permit Area; DKS: Don Kelley South General Permit Area; and TWS: Tatum Winn South General Permit Area.

inquiry: 25 January, 2018)]. Recreational harvest peaked in 1991 at 962 t and showed a general decrease through 2016 (201 t harvested in 2016) [National Marine Fisheries Service Fisheries Statistics Division, pers comm (date of inquiry: 25 January, 2018)]. A drastic increase in the number of recreational discards (released alive) from 2014 to 2016 (180%) may indicate that the stock is beginning to recover; although the quotas remain low, anglers are catching and releasing increasingly large numbers of fish. A SEDAR assessment completed in 2015 concluded that GOM gray triggerfish were no longer undergoing overfishing, but remained overfished (SEDAR-43 2015).

Although age and growth of gray triggerfish has previously been described in both the Atlantic and GOM regions (Table 1), more information is required for several reasons. First, although data from GOM natural habitats have been published (Allman et al. 2018) and incorporated widely into stock assessments, data from GOM artificial habitats have not been published and may be underrepresented in assessments. Since gray triggerfish regularly inhabit artificial reefs (Minton and Heath 1998), data

Table 1. Summary of Gulf of Mexico gray triggerfish, *Balistes capriscus*, age and growth studies. GOM = Gulf of Mexico; AARZ = Alabama Artificial Reef Zone; VBGF = von Bertalanffy growth function; par = parameter; L_∞ = mean asymptotic length, in millimeters; k = Brody growth rate coefficient, in yr^{-1}; t_0 = hypothetical age at which length equals 0, in yrs; MIA = marginal increment analysis; OTC = oxytetracycline.

Study attribute	Johnson and Saloman (1984)	Wilson et al. (1995)	Hood and Johnson (1997)	Ingram (2001)	Fioramonti (2012)	Allman et al. (2016)	Allman et al. (2018)	Present study
Study type	Age/growth, mortality	Age/growth, reproduction	Age/growth, maturity, fecundity	Movement, age/growth, reproduction, mortality	Age validation, age/growth	Age validation	Age/growth	Age/growth
Study area	Northeastern GOM	GOM	GOM	GOM	GOM	GOM	GOM; primarily West Florida Shelf	North-central GOM; primarily AARZ
n	2,808 total; 1,746 aged	318	679	1,849	3466	4	5361	1201 total; 1135 aged
Model(s) used	VBGF (3-par)	N/A	VBGF (3-par)	VBGF (3-par and 2-par); 3-par reported below	VBGF (3-par)	N/A	VBGF (3-par)	VBGF (3-par); Gompertz; Logistic
Growth parameters (all)	$L_\infty = 466$, $k = 0.38$, $t_0 = 0.19$	N/A	$L_\infty = 645$, $k = 0.15$, $t_0 = -1.90$	$L_\infty = 583$, $k = 0.18$, $t_0 = -1.58$	$L_\infty = 521$, $k = 0.27$, $t_0 = -0.12$	N/A	$L_\infty = 484$, $k = 0.34$, $t_0 =$ -0.06 yr	$L_\infty = 489$, $k = 0.57$, $t_0 = -0.27$
Growth parameters (♂)	$L_\infty = 492$, $k = 0.38$, $t_0 = 0.23$	N/A	$L_\infty = 664$, $k = 0.16$, $t_0 = -1.80$	$L_\infty = 598$, $k = 0.20$, $t_0 = -1.37$	$L_\infty = 403$, $k = 0.49$, $t_0 = -0.01$	N/A	$L_\infty = 405$, $k = 0.55$, $t_0 = 0.02$ yr	$L_\infty = 533$, $k = 0.44$, $t_0 = -0.78$
Growth parameters (♀)	$L_\infty = 438$, $k = 0.38$, $t_0 = 0.15$	N/A	$L_\infty = 421$, $k = 0.33$, $t_0 = -1.20$	$L_\infty = 514$, $k = 0.21$, $t_0 = -1.61$	$L_\infty = 381$, $k = 0.50$, $t_0 = -0.02$	N/A	$L_\infty = 387$, $k = 0.52$, $t_0 = 0.004$ yr	$L_\infty = 480$, $k = 0.44$, $t_0 = -0.78$
Max age (all)	13	11	14	9	14	N/A	14	10
Max age (♂)	13	10	14	8.1	8	N/A	9	10
Max age (♀)	12	11	10	8.8	9	N/A	10	9
Sex ratio (♂:♀)	1:1	2:1	2.1:1	1:1.04	1:1.6	N/A	1:1.6	1.07:1
Validation attempted	Yes	Yes	Yes	Yes	Yes	Yes	No	Yes
Validation method(s) and results	MIA; translucent band formation from Apr–Oct; peak Jun–Jul	MIA; translucent band forms Mar–May	OTC and MIA; could not validate opaque zone formation	MIA; translucent band forms from Dec–Feb; spawning check in Aug	OTC; one translucent zone forms in winter/early spring. MIA; same findings	OTC and MIA; this publication resulted from Fioramonti (2012); therefore, same findings	N/A	MIA; inconclusive

from artificial habitats are vital. Second, stock assessment models benefit from using the most up-to-date age data available. While the most recent published GOM study included data through the year 2013 (Allman et al. 2018), age data from 2014 to 2017 have not been published. Third, sex-specific growth parameters are needed to inform future assessment models. Sex-specific growth curves were lacking from the 2015 assessment due to the absence of sex data from fishery-dependent samples (SEDAR-43 2015). Fourth and lastly, all previous GOM gray triggerfish age and growth studies have used the von Bertalanffy growth function (VBGF) (von Bertalanffy 1938) by default, instead of considering a set of growth models in a multimodel inference or multimodel framework procedure (Katsanevakis and Maravelias 2008, Smart et al. 2016). Therefore, the goal of the present study was to use fishery-independent data collected primarily from artificial habitats to explore a suite of growth models and generate up-to-date combined and sex-specific growth curves for AARZ gray triggerfish.

Methods

Age and Growth Sampling.—Fishery-independent sampling of gray triggerfish took place during 1999–2017 in the north-central GOM (Fig. 2) and was accomplished using five different gear types: vertical longline (VL), hook-and-line, trawl, plankton purse seine, and pole-spear. Inclusion of samples from this variety of gear types helped to ensure broad coverage across size/age classes.

Adult gray triggerfish were collected during VL surveys conducted from 2010 to 2017 throughout the AARZ. Sites for VL sampling were randomly selected from a list of sites generated during sidescan sonar cruises, which covered the entire extent of the AARZ (Powers et al. 2018). Sites were sampled using bandit reels following standardized Southeast Area Monitoring and Assessment Program (SEAMAP) protocols. Briefly, monofilament backbones were fitted with either 10 or 12 gangions. Each gangion was fit with one of six circle hooks: 3/0, 8/0, 9/0, 11/0, 13/0, or 15/0; Mustad series 39960D. All hooks were baited with either Atlantic mackerel, *Scomber scombrus* Linnaeus, 1758, or cut squid (*Loligo* spp.). After each 5-min soak, catch was enumerated by species, and the lines were rotated either clockwise or counterclockwise around the vessel for the next set. Non-artificial sites (natural structure, such as rocks and rubble, as well as no structure, which consisted of sand) were also sampled. If natural reefs were identified in the sidescan sonar reports, they were automatically selected for sampling to ensure that the maximum amount of natural reef possible was sampled. Habitat types were determined using sidescan sonar data and confirmed with remotely operated vehicle (ROV) video footage. For complete details of the VL and ROV gears, refer to Gregalis et al. (2012).

Gray triggerfish were also collected through standardized fishery-independent hook-and-line surveys from 2010 to 2017 at sites inside the AARZ. Two different types of bottom tackle (“sow” and “double drop” rigs) were used. The sow rig is a single hook rig with a slip (or egg) lead, 1 m 80-lb test monofilament, and a 10/0 circle hook. The double drop is a two-hook rig with a bank sinker and an 8/0 circle hook. Rigs were baited with either cut squid (*Loligo* spp.) or Gulf menhaden, *Brevoortia patronus* Goode, 1878.

Three additional fishery-independent gear types were used to collect smaller gray triggerfish, which were not sampled with VL or hook-and-line gear. Bottom trawl

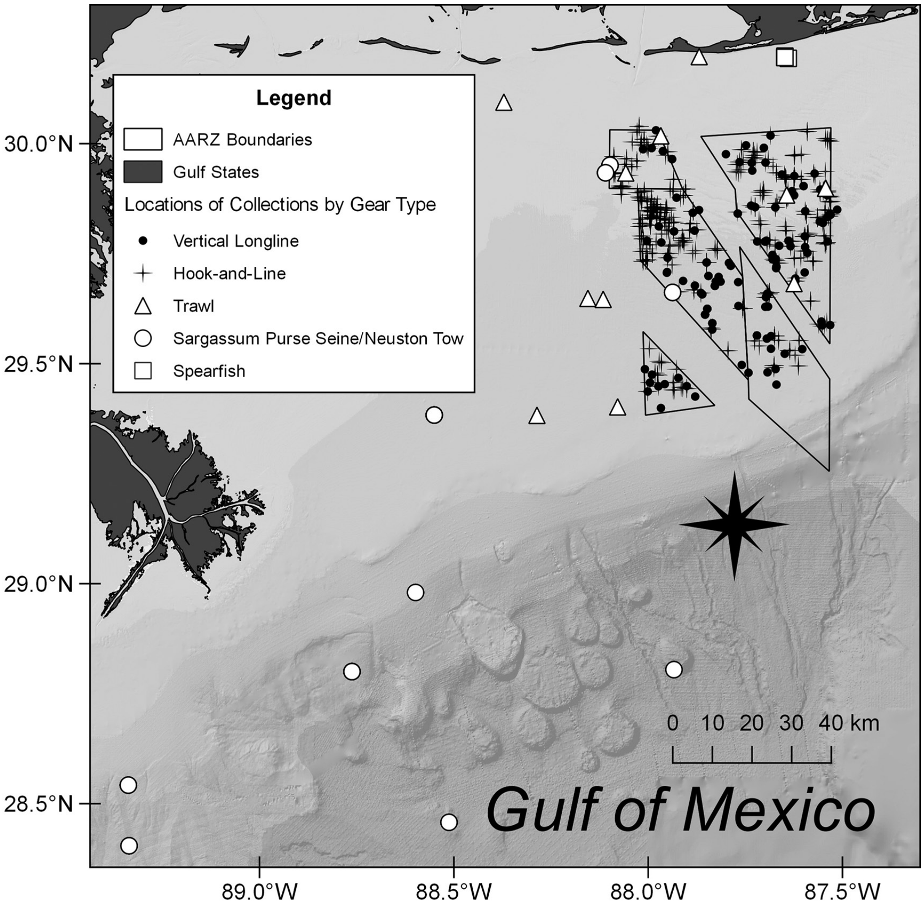

Figure 2. Collection locations of gray triggerfish, *Balistes capriscus*, sampled for age analysis using multiple gear types both inside and outside the Alabama Artificial Reef Zone from 1999 to 2017.

surveys were conducted within, and proximal to, the AARZ from 2012 to 2017. Trawling was performed using a 12.8 m semiballoon otter trawl towed at 2.5–3 knots for 30 min. Catch was sorted to species, and total biomass of each species was recorded (S Powers, University of South Alabama, unpubl data). Additionally, a 10 × 3-m plankton purse seine with 1 mm mesh and a 1 × 2-m neuston net with 1-mm mesh were used to collect juvenile fishes, including gray triggerfish, within holopelagic *Sargassum* mats. Sampling was conducted during 1999, 2000, 2002, 2010, and 2011 at sites within and outside the AARZ (Hoffmayer et al. 2005, Kramer 2014). Lastly, gray triggerfish were collected in 2016 and 2017 by spearfishing near Orange Beach, Alabama (30.2697°N, 87.5868°W), outside of the AARZ. All gray triggerfish from these surveys were sampled to augment the size distribution available for analysis.

Each fish was weighed to the nearest kilogram (VL and hook-and-line gears) or gram (trawl, plankton purse seine, and pole-spear gears) and measured to the nearest millimeter (total length, fork length, natural total length, and stretch total length). The first dorsal spine of each fish was extracted using the methods of Ingram (2001) and stored frozen for later age analysis. Gonads were extracted and weighed to the nearest 0.001 g, and each fish was sexed macroscopically.

Several specimens were so small that they had not yet developed a fork in the caudal fin; therefore, fork length was not directly measured. For trawl-sampled fish that had both fork and standard-length measurements, fork length was regressed on standard length, resulting in the equation:

$$\textit{Fork Length} = 1.16\ (\textit{Standard Length}) + 6.42, \qquad \text{(Eq. 1)}$$

where fork and standard lengths are expressed in millimeters (n = 13, R^2 = 0.998). This regression was used to estimate the fork lengths for trawl samples lacking a fork length measurement. For gray triggerfish sampled from *Sargassum*, fork length was assumed to equal total length because the caudal shape is truncated during this early life stage.

Spine Processing.—Prior to aging spines, a set of annotated dorsal spine images was reviewed for training purposes (Fioramonti and Allman 2012). Additionally, the Gulf States Marine Fisheries Commission gray triggerfish reference set of 115 dorsal spine sections (Fioramonti and Allman 2012) was aged and compared to accepted reference ages to ensure aging methods were consistent.

Spine preparation and sectioning followed Allman et al. (2016). Spine sections were viewed with transmitted light under 10–32× magnification. A photograph of each spine section was generated at 6.3× magnification using the program Image-Pro Plus (Media Cybernetics Inc. 2007). For each fish, the best of the three spine sections was selected for aging. The number of translucent zones in the spine section, including any partially-formed zones on the margin, was counted and recorded as the age of the fish. The margin was assigned a code of 1 or 2, where 1 = translucent zone on the edge and 2 = opaque material present between the last translucent zone and the section edge. For all spines assigned an age of 1 yr or greater (excluding age-0 fish because margin type could not be determined), the percentage of spines with translucent margins was examined in relation to the month of capture to determine if translucent zones are deposited on an annual cycle. Each spine was assigned one of the following readability codes: good (G), readable (R), difficult (D), unreadable (U), or unreadable due to poor processing (P). Spines assigned a code of U or P were omitted from further age analysis. All fish were aged without knowledge of fish length. After the primary reader completed all first reads, two additional experienced readers completed second reads on one random selection of 18% of the spine sections. Average percent error (APE) was calculated to estimate reader precision (Beamish and Fournier 1981, Campana 2001). Since APE averages precision across age groups (i.e., does not test for differences in precision at different ages), a chi-square test of symmetry was conducted to determine if differences between readers were systematic or due to random error (Hoenig et al. 1995). Second reads served only to check APE; first reads were used as final ages.

Modeling Growth Parameters.—A multimodel framework was used to investigate a suite of candidate growth models and determine the best function (Katsanevakis and Maravelias 2008, Smart et al. 2016). The VBGF, Gompertz model (Gompertz 1825), and logistic model (Ricker 1975) were fit to the entire data set, which consisted of all gray triggerfish age data (female, male, and unknown sexes) pooled together. The unknown sex observations were included in this analysis because they

Table 2. Gray triggerfish, *Balistes capriscus*, summary statistics by gear type.

Gear type	Spines collected	Fork length (mm) Range	Fork length (mm) Mean (SE)	Age (yrs) Range	Age (yrs) Mean (SE)	Sex ratio (♂:♀)
Vertical longline	175	297–617	449 (5.55)	2–10	4.18 (0.12)	1.36:1
Hook-and-line	850	243–605	423 (2.21)	1–9	3.64 (0.05)	1.04:1
Purse seine/neuston tow	138	22–157	60 (2.39)	0–1	0.02 (0.01)	Unknown
Spearfishing	22	133–233	172 (6.02)	0–1	0.64 (0.10)	1:1.43
Trawl	16	78–320	165 (16.74)	0–3	0.93 (0.21)	1:2.50
All	1,201	22–617	377 (2.39)	0–10	3.25 (0.31)	1.07:1

represented the juvenile (age-0) fish critical for anchoring the growth curve. Akaike's information criterion (AIC; Akaike 1973, Katsanevakis and Maravelias 2008) was used to rank the models with respect to their fit. The model with the smallest AIC value was chosen as the best-fitting model.

To provide a basis for comparison with other published studies, sex-specific growth parameters were modeled using the VBGF. Eight different versions of the VBGF were fit to the data: a general version, which allowed all three parameters (L_∞, k, and t_0) to vary between sexes; three versions which allowed two of the three parameters to differ between sexes while holding the third constant between sexes; three versions which allowed only one parameter to differ between sexes while holding the other two constant between sexes; and a common version, which held all three parameters constant between sexes (Nelson et al. 2018). AIC was used to rank the model versions based on fit and to choose the best model among the candidate models. A likelihood ratio test was used to compare the resulting male and female growth models and generate a P-value based on the differences between the nested models, where a P-value of <0.05 indicates differences between the models (Kimura 1980). All growth parameters were modeled in the R language and software environment v3.3.1 (R Core Team 2016) using the add-on packages FSA, v0.8.12 (Ogle 2017) and nlstools (Baty et al. 2015). Maps were generated using Quantum GIS v2.14.7 (Quantum GIS Development Team 2017).

Results

Age and Growth Samples.—A total of 1201 individual gray triggerfish were sampled for aging (Table 2). Most fish were collected via the hook-and-line gear type ($n = 850$). A total of 496 sampled fish were identified as female, 532 as male, and 173 as unknown sex (most of the unknowns were small, *Sargassum*-associated juveniles). The male to female ratio was 1.07:1 and did not significantly differ from a 1:1 ratio ($\chi^2 = 1.26$, df = 1, $P = 0.26$). While samples were collected as early as 1999 and during each month except January, most were collected between 2014 and 2017 (80%) and during the months of April and May (60%). Most were collected from unknown artificial structure; of the known structure types, the highest numbers of spines were collected from chicken transport devices and pyramids. Fish were primarily collected between 20 and 40 m depth.

Fork length of sampled fish ranged from 22 to 617 mm (mean 377, SE 2.39), with nearly 50% of fish measuring between 350 and 450 mm fork length (Fig. 3). A Kolmogorov-Smirnov test revealed significant differences in fork length between

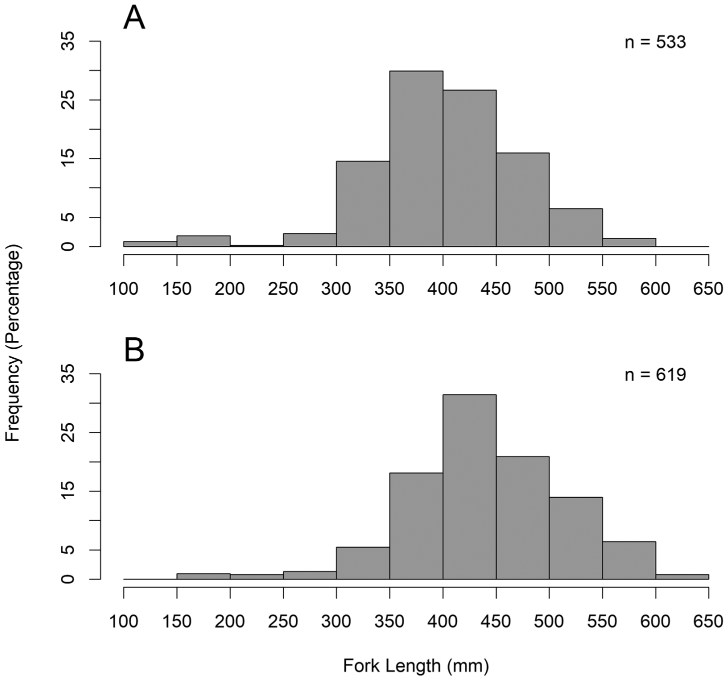

Figure 3. Length frequency distributions for (A) female and (B) male gray triggerfish, *Balistes capriscus*, sampled for age analysis.

male and female samples (D = 0.26, $P < 0.01$), with larger males noted on average. The length-weight relationship was expressed by the equation:

$$Weight = 1 \times 10^{-8} \, (Fork\ Length)^{3.08}, \qquad \text{(Eq. 2)}$$

where weight is expressed in kilograms and fork length is expressed in millimeters.

Spine Aging.—Sixty-six spines (5.5%) were deemed unreadable due to deformities or poor processing and were omitted from further analysis. As a result, 1135 spines were available for age analysis, and 988 (87%) had accompanying sex data. Among the 1135 readable spines, 128 were assigned an age of 0 yrs, and these were not included in the edge type analysis because an edge type could not be assigned. Spine sections varied in shape, clarity, and readability (Fig. 4A–F). The APE for the 223 randomly selected spine sections that were assigned both first and second reads was 11%. The chi-square test of symmetry revealed that differences between the two readers were due to random error ($\chi^2 = 22.47$, df = 18, $P < 0.01$). Edge analysis revealed variable percentages of translucent margins throughout the calendar year with a maximum value in July (Table 3).

The average age of all observations was 3.25 (SE 0.31) yrs (Table 2). Vertical longline and hook-and-line gear types collected the oldest fish, on average, with respective mean ages of 4.18 (SE 0.12) and 3.64 (SE 0.05) yrs. Males attained a maximum age of 10 yrs, and females, 9 yrs. A Kolmogorov-Smirnov test showed that the female and male age distributions were significantly different (D = 0.10, $P = 0.02$), with males reaching older ages compared to females. Seven-hundred-and-seventeen of

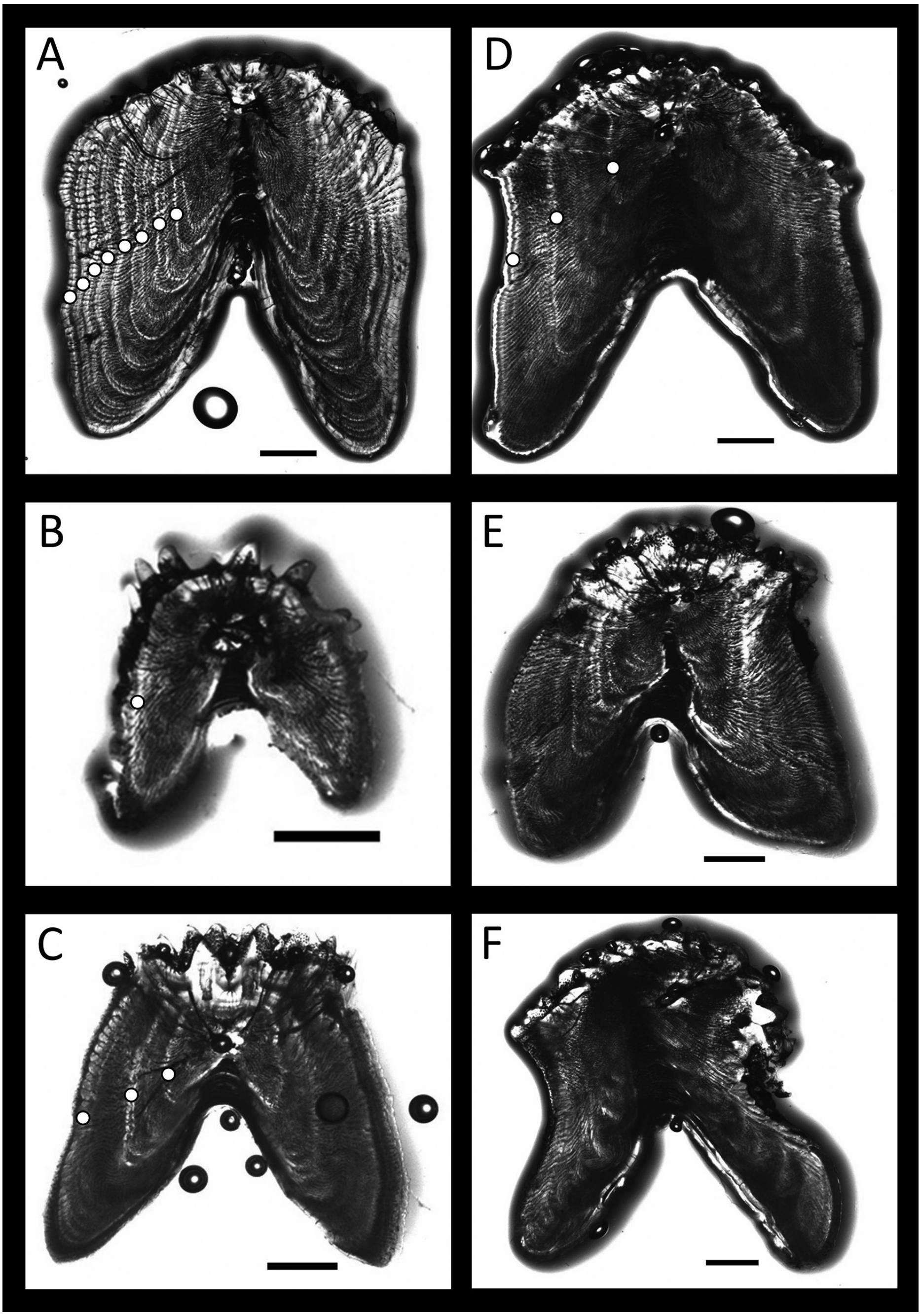

Figure 4. Images of gray triggerfish, *Balistes capriscus*, spine sections demonstrating the range in size, shape, and quality of sections. The scale bar on each image represents 1 mm. (A–C) Examples of easily readable sections assigned a score of "G" (good). (D) Example of a readable section assigned a score of "R" (readable). (E) Example of a readable, but challenging, section assigned a score of "D" (difficult). (F) Example of a deformed, unreadable spine assigned a score of "U" (unreadable). Translucent zones for good and readable spines (A–D) are designated by white circles.

Table 3. Results of edge type analysis for *Balistes capriscus*. Sample size indicates the number of spines with an assigned edge type.

Attribute	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
n	N/A	N/A	5	237	567	6	22	68	169	17	32	3
Translucent	N/A	N/A	40%	67%	69%	33%	77%	52%	20%	53%	9%	33%

the measured and aged gray triggerfish were collected from artificial habitat, while 22 were collected from natural habitat. Kolmogorov-Smirnov tests revealed that fork length was similar (D = 0.182, P = 0.482) and age was also similar (D = 0.135, P = 0.834) between artificial and natural habitats.

Growth Parameters.—The multimodel framework procedure, during which the three candidate growth models (VBGF, Gompertz, and logistic) were compared, showed little variation in the shapes of the growth curves (Fig. 5A). The VBGF resulted in the best fit as measured by AIC (AIC = 12,425; ΔAIC = 0) with the Gompertz (ΔAIC = 17.61) and logistic (ΔAIC = 43.77) models producing substantially lower quality fits. Therefore, the VBGF was determined to be the best-fitting model for the entire age data set (Table 4). Visual inspection of the residual plots indicated that the residuals were approximately normally distributed, further supporting the VBGF as the best-fitting model. The VBGF equation for all observations is:

$$l_t = 488.63(1 - e^{-0.57(t-(-0.27))}). \quad \text{(Eq. 3)}$$

Since the VBGF best fit the age data for all observations, further modeling, during which growth parameters were compared between males and females, was performed using only the VBGF. During the sex-specific modeling procedure, the "fit2L" version of the VBGF (the version which allowed the L_∞ parameter to vary by sex while holding k and t_0 constant) was ranked the best-fitting model when considering AIC value. The "fit2L" version was closely followed by the version "fit1Lk" (ΔAIC = 1.5), which allowed L_∞ and k to vary by sex while holding t_0 constant, and the version "fit1LT" (ΔAIC = 1.6), which allowed L_∞ and t_0 to vary by sex while holding k constant. Based on the model summary, females have a lower L_∞ (480.26, SE 7.99) compared to males (532.89, SE 8.95). Both sexes share the same k (0.44, SE 0.04) and t_0 (−0.78, SE 0.16) parameters (Table 4, Fig. 5B). The VBGF equations for females and males are:

$$\text{Females: } l_t = 480.26(1 - e^{-0.44(t-(-0.78))}) \quad \text{(Eq. 4)}$$

$$\text{Males: } l_t = 532.89(1 - e^{-0.44(t-(-0.78))}) \quad \text{(Eq. 5)}$$

Table 4. Parameter estimates for the von Bertalanffy growth functions (VBGF) for combined (sexes pooled, including unknown sex) and sex-specific gray triggerfish, *Balistes capriscus*, age data. L_∞ = mean asymptotic length, in millimeters; k = Brody growth rate coefficient, in yr^{-1}; t_0 = hypothetical age at which length equals 0, in yrs.

Model	L_∞ (SE)	k (SE)	t_0 (SE)
VBGF (all data combined)	488.63 (5.19)	0.57 (0.02)	−0.27 (0.03)
VBGF (♀)	480.26 (7.99)	0.44 (0.04)	−0.78 (0.16)
VBGF (♂)	532.89 (8.95)	0.44 (0.04)	−0.78 (0.16)

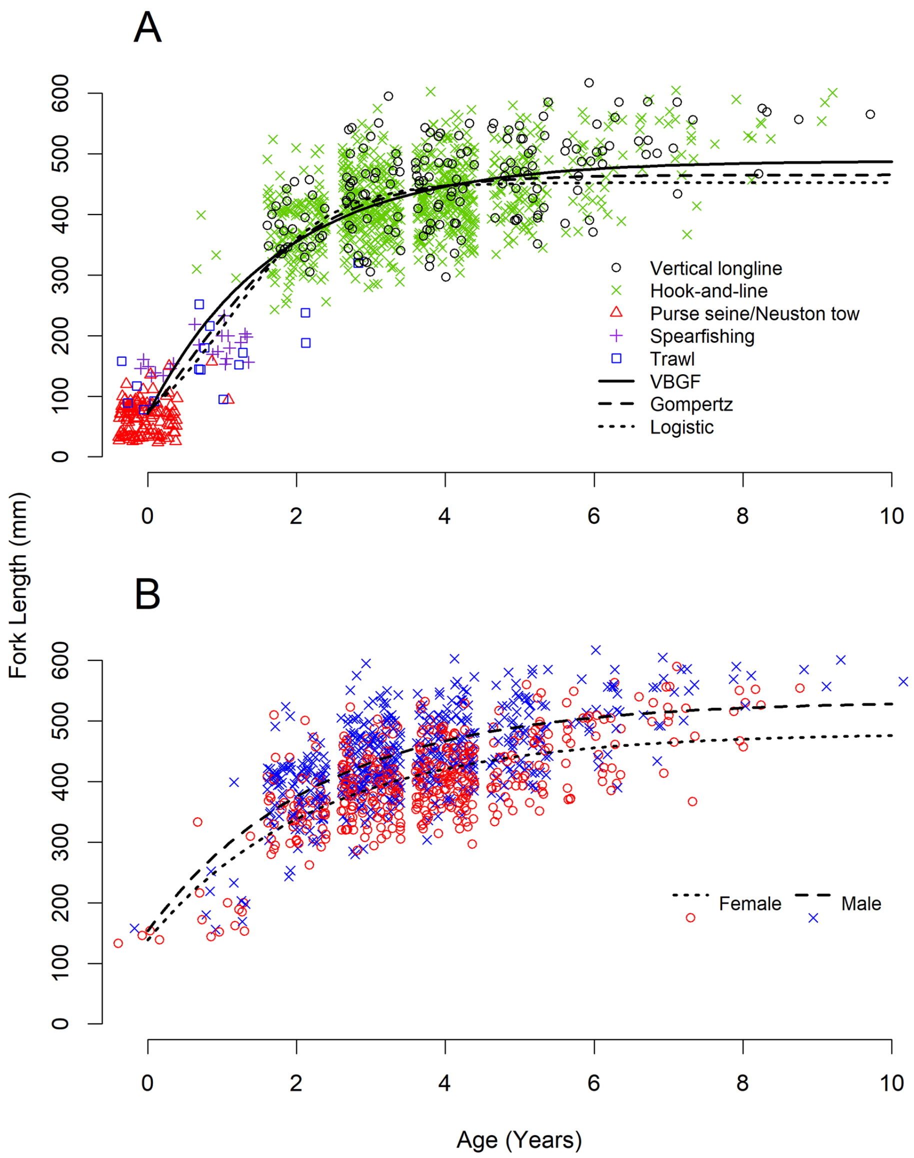

Figure 5. (A) Results of the multimodel framework approach. Each point represents the length and age data for a single gray triggerfish, *Balistes capriscus*. (B) Gray triggerfish sex-specific von Bertalanffy growth function.

A likelihood ratio test revealed that the VBGF growth parameters are significantly different between female and male gray triggerfish (χ^2 = 149.86, df = 1, P < 0.01). Mean size-at-age differed significantly between sexes for six of the eight ages that possessed sample sizes large enough to make comparisons (Table 5).

Table 5. Mean size-at-age comparison between male and female gray triggerfish, *Balistes capriscus*.

Age	♀	♂	♀ mean size (mm)	♂ mean size (mm)	*t* value	df	*P* value	Similar/ different
0	4	1	143.00	158.00	N/A	N/A	N/A	N/A
1	12	9	201.33	223.22	−0.73	15.45	0.47	Similar
2	64	101	357.02	389.13	−4.05	129.38	<0.01	Different
3	133	166	392.47	434.64	−6.88	293.77	<0.01	Different
4	157	119	411.80	457.51	−7.12	235.09	<0.01	Different
5	53	70	429.57	476.13	−4.75	113.70	<0.01	Different
6	30	22	457.87	512.59	−3.52	45.83	<0.01	Different
7	15	14	504.40	538.86	1.79	26.62	0.09	Similar
8	7	4	514.00	564.75	−2.54	8.13	0.03	Different
9	1	3	601.00	581.00	N/A	N/A	N/A	N/A
10	0	1	N/A	565.00	N/A	N/A	N/A	N/A

Discussion

The present study represents a comprehensive assessment of gray triggerfish age and growth across an expansive network of artificial reefs. The maximum age assigned to male gray triggerfish was 10 yrs, and the maximum age assigned to females was 9 yrs. These ages are at the low end of the previously observed maximum ages in the GOM, which range from 9 yrs (Ingram 2001) to 14 yrs (Hood and Johnson 1997, Fioramonti 2012, Allman et al. 2018). The similarity in maximum age between Ingram (2001) and our study is likely due to overlap in sampling region between the two studies; both studies sampled primarily from the AARZ. In contrast, the younger maximum ages observed in our study as compared to previous GOM studies is likely due to differences in fishing pressure. Fishing pressure is probably greater on the artificial reefs present in the AARZ than on the natural reef sites sampled in the other studies, which may be located in deeper waters and less accessible to recreational anglers.

The multimodel framework used in the present study to evaluate the suitability of three different length-at-age functions is a novel approach to investigating GOM gray triggerfish age and growth. This approach is preferable to modeling age and growth using only the VBGF because it enables the investigator to choose the best-fitting model from a series of models. In this case, the VBGF outperformed the other candidate models and provided the best fit to the size-at-age data in our study, and was therefore used to represent growth. Once selected, several different versions of the VBGF were fit to the data. These versions permitted various combinations of the three parameters to vary by sex, instead of carrying the assumption that all three parameters should vary by sex. This approach allowed for customized growth models.

The combined L_∞ estimate from the present study is considerably smaller than the L_∞ estimate from some previous GOM studies, particularly Hood and Johnson (1997) and Ingram (2001) (Table 1). This suggests that gray triggerfish from the AARZ may reach smaller maximum sizes compared to gray triggerfish on a gulf-wide scale. Conversely, the maximum size of gray triggerfish may be approximately the same across the GOM, but AARZ gray triggerfish may be less likely to reach that maximum size due to concentrated fishing pressure, which often selects for decreased size-at-age (Zhao et al. 1997). The observed differences in L_∞ could also be attributed to differences in the numbers of small and large fish between the studies. The k estimate from the present study is greater than the k estimates from all previous GOM studies (Johnson and Saloman 1984, Hood and Johnson 1997, Ingram 2001, Fioramonti 2012, Allman et al. 2018). These results imply that AARZ gray triggerfish reach their maximum size faster than other GOM gray triggerfish. This elevated growth rate could result from the plethora of artificial reefs present in the AARZ. These artificial habitats might permit gray triggerfish to grow rapidly and thrive in this portion of the north-central GOM. Alternatively, a non-environmental explanation for the elevated growth rate involves the modeling process. The higher k estimate may result from the abundance of age-0 gray triggerfish used to model growth (Allman et al. 2018). Specifically, age-0 data tend to anchor the curve, which may result in a higher, more accurate k estimate compared to studies that incorporate few young fish into the model. For example, Burton et al. (2015) fixed $t_0 = 0$ to account for a lack of age-0 fish, which pulled the curve downward to an intercept of (0, 0), doubled the original k estimate due to the steeper slope, and produced more realistic length at age estimates for young fish.

The results of the sex-specific modeling procedure suggest sexual dimorphism; specifically, that males have a significantly larger L_∞ parameter estimate compared to females (Table 4), as noted by Allman et al. (2018). Five previous age and growth studies for GOM gray triggerfish reported sex-specific parameters, and in all five studies, the L_∞ estimate for males was larger than for females (Johnson and Saloman 1984, Hood and Johnson 1997, Ingram 2001, Fioramonti 2012, Allman et al. 2018). Comparisons of size-at-age also show greater size-at-age in males compared to females at ages 2 through 6 and 8 (Table 5). The fact that males appear to reach greater maximum lengths than females is likely due to reproductive behavior. Simmons and Szedlmayer (2012) observed that male gray triggerfish are significantly larger than females, build and defend nest sites, and maintain a harem of females during the spawning period. Larger size in males may confer an advantage because larger males may be better able to attract a harem and defend nests from predators (Côte and Hunte 1989).

In the present study, spines from 138 gray triggerfish caught in *Sargassum* were sectioned and aged. The resulting ages confirmed that gray triggerfish inhabiting *Sargassum* are, in fact, age-0 individuals; until now, this was only assumed. In many sectioned spines of gray triggerfish sampled from *Sargassum* (43 of 116 readable spines), a circular translucent ring was visible close to the focus. This ring was also apparent in many spines collected from settled gray triggerfish (625 of 1136 readable spines). Nearly all (114 of 116) of the readable *Sargassum* gray triggerfish were assigned an age of 0 yrs; the remaining two were aged as 1 yr. This assessment of *Sargassum* ages is supported by Simmons and Szedlmayer (2011), who reported that gray triggerfish remain in the plankton for 4–7 mo. Since all *Sargassum* gray triggerfish should theoretically be age-0, if a focal ring was present in a spine section, it was not counted as an annulus. Additionally, the measured distance between a focal ring and the focus of a section was consistently too small (<1 mm) to consider the focal ring an annulus. A focal ring was noted by Ingram (2001) and was termed a "settlement check" because it was assumed to represent the transition from *Sargassum* to benthic habitats. However, the focal ring noted in the *Sargassum* gray triggerfish aged in our study cannot represent such a transition. Several mechanisms could be responsible for the formation of this ring. It could represent the transition from benthic eggs to pelagic *Sargassum*, or from larval to juvenile stages, which has been shown in other species moving to drift algae (Kingsford and Milicich 1987, Rogers et al. 2001). It could also represent a response to an environmental trigger, such as a change in sea surface temperature. The most likely explanation is that the focal ring results from a shift in gray triggerfish diet, perhaps as gape size increases, while the juveniles are residing in the *Sargassum*.

Gray triggerfish spines are inherently difficult to age, and this is reflected by our relatively high APE value (11%). An APE of ≤5% is frequently used as a reference point for moderately long-lived species aged using otoliths (Campana 2001), yet the APE in the present study is similar to APEs reported in other recent gray triggerfish age and growth studies, all of which used the first dorsal spine for aging. For instance, Burton et al. (2015) reported an APE of 11%, Kelly-Stormer et al. (2017), 12%, and Allman et al. (2018), 10.8%. One issue intrinsic to species aged using spines is the process of resorption; if annuli near the spine core are resorbed, the reader could potentially underestimate the age of the fish (Casselman 1983). In the present study, resorption may have caused the models to inadequately estimate size-at-age in the older fish. However, Ingram (2001) reported that the focal ring or "settlement check" was the only mark affected by resorption in older gray triggerfish, and Moore (2001) argued that the relatively short lifespan of gray triggerfish frees the species from difficulties associated with aging older fish due to resorption. Based on these observations, and the lack thereof from other gray triggerfish studies, resorption does not appear to be a significant issue in aging this species. Nonetheless, future fieldwork involving conventional tagging or oxytetracycline marking of young-of-year gray triggerfish could help determine, with more certainty, the extent to which resorption impacts age and growth studies for this species.

In the edge analysis component of our study, the highest percentage of translucent margins was observed in July (77.27%). No gray triggerfish were collected in January, and all February gray triggerfish were assigned an age of 0 yrs and thus had no recorded margin type. Consequently, the months of January and February were not included in the edge type analysis. The percentage of translucent margins varied considerably throughout the calendar year and there was no clear pattern in the timing of translucent zone (annulus) formation. This could be due to the relatively small sample sizes for some months. Previous GOM studies have noted two annual peaks corresponding to a prominent winter/spring growth zone (annulus) and a less-defined summer zone (spawning zone), thought to be due to limited feeding activity during the spawning season (Ingram 2001, Allman et al. 2016).

Although previous studies in both the Atlantic Ocean and GOM have determined annual periodicity in translucent zone formation via marginal increment and edge analyses, the range of reported results is broad. Escorriolia (1991) reported that one translucent zone (annulus) forms each year, but did not indicate timing. Ingram (2001) stated that annuli form during the winter. Allman et al. (2016) reported that annuli form during winter to early spring. Moore (2001) found that annuli form during the spring, while Wilson et al. (1995), Burton et al. (2015), and Kelly-Stormer et al. (2017) reported that annuli form in the late spring to early summer, and Johnson and Saloman (1984) noted summer formation. Lastly, Bernardes (2002) reported that annuli form during both summer and winter. These inconsistencies indicate that marginal increment and edge analyses, which were called into question nearly two decades ago by Campana (2001), may be unreliable validation methods for determining the temporal nature of annulus deposition in gray triggerfish. However, annual formation of translucent zones has been validated in the dorsal spines of captive reared gray triggerfish held under natural conditions (Allman et al. 2016).

The over-exploitation of targeted GOM reef fish stocks is not a new problem and remains an important issue. Up-to-date information about the GOM gray triggerfish population is required to successfully manage the stock. The present study's comprehensive sex-specific growth curves, modeled using fishery-independent samples collected from artificial habitats, suggest sexual dimorphism and provide an important source of data for assessing the GOM gray triggerfish stock.

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