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Abstract—Gray triggerfish (*Balistes capriscus*) sampled from recreational and commercial vessels along the southeastern coast of the United States in 1990–2012 (n=6419) were aged by counting translucent bands on sectioned first dorsal spines. Analysis of type of spine edge (opaque or translucent) revealed that annuli formed during March–June, with a peak in April and May. Gray triggerfish were aged up to 15 years, and the largest fish measured 567 mm in fork length (FL). Weight–length relationships from a different set of sampled fish were $\ln(W)=2.98\times\ln(FL)-17.5$ (n=20,431; coefficient of determination [r^2]=0.86), ln-transform fit; $W=3.1\times10^{-5}\ TL^{2.88}$ (n=7618), direct nonlinear fit; and $FL=30.33+0.79\times TL$ (n=8065; r^2=0.84), where W=whole weight in grams, FL=fork length in millimeters, and TL=total length in millimeters. Mean observed sizes at ages 1, 3, 5, 10, and 15 years were 305, 353, 391, 464, and 467 mm FL, respectively. The von Bertalanffy growth equation for gray triggerfish was $L_t=457\ (1-e^{(-0.33(t+1.58))})$. Natural mortality ($M$) estimated by Hewitt and Hoenig's longevity-based method that integrates all ages was 0.28. Age-specific M values, estimated with the method of Charnov and others, were 0.65, 0.45, 0.38, 0.34, and 0.33 for ages 1, 3, 5, 10, and 15, respectively. Gray triggerfish recruited fully to recreational fisheries by age 4 and to the commercial fishery by age 5. Estimates of total mortality averaged 0.95 across all fisheries for the years 1986–2011.

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The gray triggerfish (*Balistes capriscus*) (family Balistidae) is widely distributed throughout the Atlantic, from Nova Scotia to Argentina and throughout the Gulf of Mexico in the western Atlantic (Briggs, 1958; in Moore, 1967) and, in the eastern Atlantic, from Ireland (Quigley et al., 1993) to southwestern Africa (Longhurst and Pauly, 1987; Kortenang et al., 1996), where tremendous increases in biomass have been observed for this species beginning in the late 1960s (Caveriviere, 1982; Ofori-Danson, 1989). Gray triggerfish exhibit reproductive behavior that is benthic and nest-building (MacKichan and Szedlmayer, 2007; Simmons and Szedlmayer, 2012), and larvae and juveniles have been shown to use drifting mats of brown algae (*Sargassum* spp.) for habitat in the Gulf of Mexico (Wells and Rooker, 2004) and off the Atlantic coast of the United States (Settle, 1993), generally settling out of the pelagic zone to benthic habitats at age 0 and at a mean size of 96 mm in fork length (FL) in the fall (October) (Simmons and Szedlmayer, 2011).

Gray triggerfish are of major importance to the commercial and recreational sectors of the fishery for reef fishes in the southeastern United States (SEUS). Within the recreational sector, estimated annual landings from headboats sampled by the Southeast Region Headboat Survey (SRHS), which is administered by the Beaufort Laboratory of the Southeast Fisheries Science Center (SEFSC), National Marine Fisheries Service (NMFS), averaged 56 metric tons between 1986 and 2011 (Brennan[1]). These landings have equated to an average ranking of sixth among the 73 species managed under the South Atlantic Fishery Management Council's (SAFMC) Snapper-Grouper Fishery Management Plan. Estimated landings from private recreational boats and charter boats, the other component of the recreational sector, averaged 84.5 metric tons annually during 1986–2011 (Sminkey[2]). Commercial fisheries of the SEUS harvested an average of 125.5 met-

[1] Brennan, K. 2013. Unpubl data. Southeast Fisheries Science Center, National Marine Fisheries Service, Beaufort, NC 28516-9722.

[2] Sminkey, T. 2013. Unpubl. data. National Marine Fisheries Service, NOAA, Silver Spring, MD 20910.

ric tons of gray triggerfish annually during 1986–2011 (Gloeckner[3]). Landings are widely distributed along the East Coast of the United States, from North Carolina to southeast Florida. The Florida Keys account for very little in the way of gray triggerfish landings; headboat landings have averaged only 135 kg annually from 1986 to 2011. In terms of rankings of the 2 fishery sectors, the recreational fishery ranks first, averaging 54.6% of the annual catch during 1986–2011, followed by the commercial sector (45.4%).

Gray triggerfish are currently managed by the SAFMC with a minimum size limit of 305 mm (12 in) in total length (TL) in commercial and recreational fisheries off the eastern coast of Florida only and with a daily aggregate bag limit of 20 snappers or groupers per person for recreational fishermen (SAFMC[4]). Commercial harvest of gray triggerfish closes once the annual catch limit has been reached and until the new fishing year begins (for example, this fishery re-opened on 1 January 2014).

Published studies on the aspects of life history of gray triggerfish from the eastern Atlantic include growth (Ofori-Danson, 1989; Aggrey-Fynn, 2009) and reproduction (Ofori-Danson, 1990) studies from Ghana. Studies from the western Atlantic, in addition to the ones previously mentioned, include an age and growth study from Brazilian waters (Bernardes, 2002), 3 unpublished college theses in which the life history characteristics of populations off the SEUS coast or GOM were examined (Escorriola, 1991; Ingram, 2001; Moore, 2001), and a single published age and growth study from the Gulf of Mexico (Johnson and Saloman, 1984).

We studied gray triggerfish from the SEUS because this species is an important resource for all reef fisheries in the SEUS; however, little new biological information has been provided in recent years. Furthermore, updated information on the life history parameters of this fish is needed because NMFS is undertaking the first comprehensive stock assessment of gray triggerfish collected from the Atlantic waters off the SEUS. This study provides information on life history parameters of gray triggerfish collected from the commercial and recreational fisheries of the SEUS and provides a comparison of the new parameter estimates with those from previous life history studies conducted in the SEUS and other areas.

Materials and methods

Age determination

Gray triggerfish were opportunistically sampled from fisheries landings along the SEUS coast from 1990 to 2012 by port agents employed by the SRHS and the SEFSC Trip Interview Program (TIP) to sample commercial fisheries landings. The majority of specimens from both fishery sectors were captured by conventional vertical hook-and-line gear. A small number of fish (n=5) were obtained from fishery-independent sampling that was conducted in Florida with traps used in the black sea bass fishery. Measurements of FL and TL of specimens were recorded in millimeters. Whole weight (W) was recorded for fish landed in the headboat fishery. Fork lengths were measured for all specimens as standard protocol, but not all fish were weighed or measured for TL; therefore, weight–length relationships may have different sample sizes. Fish landed commercially were eviscerated at sea; therefore, whole weights were unavailable. Because of predetermined sampling protocols and time constraints imposed by their workload, samplers were unable to determine the sex of fishery-dependent specimens.

First dorsal spines were removed from 6419 gray triggerfish and stored dry in coin envelopes. Spines were used as aging structures instead of otoliths because gray triggerfish otoliths are small and difficult to extract. Spines were sectioned with a low-speed saw, according to the methods of Potts and Manooch (1995). A single 0.5-mm section was taken from the spine above the condyle. The sections were mounted on microscope slides with thermal cement and covered with mounting medium. Then, the sections were viewed under a dissecting microscope at 12.5× magnification with transmitted light. Each sample was assigned a ring count equal to the number of translucent zones.

Three readers interpreted gray triggerfish spine sections. Two readers (JCP and MLB) each read a separate portion (45%) of the sections, and a third reader (MC) read the other 10%. To ensure consistency among readers in the interpretation of growth structures, each individual read a calibration set of 100 spine sections, and the 2 primary readers each read an additional set of 98 spine sections, for the calculation of an index of average percent error (APE), by following the method of (Campana, 2001).

Increment periodicity was assessed with edge analysis. The edge type of the spine was noted: 1=translucent zone forming on the edge of the spine section; 2=narrow opaque zone on the edge, generally <30% of the width of the previous opaque zone; 3=moderate opaque zone on the edge, generally 30–60% of the width of the previous opaque zone; 4=wide opaque zone on the edge, generally >60% of the width of the previous opaque zone. On the basis of edge frequency analysis, all samples were assigned a chronological, or calendar, age obtained by increasing the translucent zone count by one if the fish was caught before that increment was formed and had an edge with an opaque zone that was moderate to wide (type 3 or 4). All fish caught after translucent zone formation would have a chronological age equivalent to the translucent zone count.

[3] Gloeckner, D. 2013. Unpubl. data. Southeast Fisheries Science Center, National Marine Fisheries Service, Miami, FL 33149.

[4] SAFMC (South Atlantic Fishery Management Council). 2014. Fish ID and regs: gray triggerfish. http://www.safmc.net/fish-id-and-regs/gray-triggerfish, accessed 10 November 2014.

Growth

Von Bertalanffy (1938) growth parameters were estimated from the observed length-at-age data. The chronological age of the fish was adjusted for the time of year caught (Mo_c), therefore, creating a fractional age (Age_f) from the chronological age (Age_c) on the basis of a July 1 birth date (Mo_b):

$$Age_f = Age_c + ((Mo_c - Mo_b)/12). \quad (1)$$

This birth date was selected on the basis of reproductive studies that show that peak spawning of gray triggerfish occurs during June–July in waters off the SEUS (Moore, 2001) and in the GOM (Simmons and Szedlmayer, 2012). Parameters were derived with the PROC NLIN procedure and the Marquardt option in SAS[5] statistical software, vers. 9.3 (SAS Institute, Inc., 1987). A Student's t-test ($P<0.05$) was used to detect if there were significant differences in mean sizes between sectors for the purpose of determining whether pooling of data across sectors was appropriate. We also performed an analysis of covariance (ANCOVA) of length-at-age data by sector (recreational versus commercial), using age as the covariate, to determine whether pooling of data was appropriate (i.e., there were no significant differences in length at age by sector).

Weight–length relationships

We regressed fish whole weight (W, in grams) on fish FL (in millimeters, n=20,431) and TL (in millimeters, n=7618), using data for all gray triggerfish measured by the SRHS from 1972 to 2010 and not just those fish sampled for aging structures. Total length was not measured for many of the fish, and some fish were not weighed. The fish used for age analysis (n=6419) were a subset of the total number of gray triggerfish measured by the SRHS (n=20,431). We regressed FL on TL (n=8065), also with the SRHS data set. For all relationships, we evaluated both a nonlinear fit, using nonlinear least squares estimation in SAS software (SAS Institute, Inc., 1987), and a linearized fit of the log-transformed data, examining the residuals to determine which regression was appropriate.

Total mortality

Age-length keys (Ricker, 1975) were developed for 25-mm intervals by using all aged specimens and the calculation of the age distribution (measured as a percentage) for each interval. Age frequencies for unaged fish by sector were developed with age-length keys (for aged fish) weighted by annual landings from the respective sector and length frequencies (for unaged fish); data for both the landings and length frequencies were acquired from the SRHS, the NMFS Marine Recreational Information Program (MRIP) for samples from recreational fishermen other than those on headboats, and the SEFSC TIP. To optimize the accuracy and precision of our estimates, we ensured that we met the criteria of Coggins et al. (2013) with respect to total sample size (500–1000) and number of aged fish per length bin (at least 10 fish per bin).

Total instantaneous mortality rates (Z) were estimated by using catch curve analysis (Beverton and Holt, 1957). Only fully recruited ages (modal age+1) were used to estimate Z because the age group at the top of the catch curve may not be fully vulnerable to the fishing gear (Everhart et al., 1975).

Natural mortality

We estimated the instantaneous rate of natural mortality (M) using 2 methods.

1) Hewitt and Hoenig's (2005) longevity mortality relationship:

$$M = 4.22/t_{max}, \quad (2)$$

where t_{max} is the maximum age of the fish in the sample;

2) Charnov et al.'s (2013) method, where von Bertalanffy growth parameters are used:

$$M = (L/L_\infty)^{-1.5} \times K, \quad (3)$$

where L_∞ and K are the von Bertalanffy growth equation parameters (asymptotic length and growth coefficient); and

$$L = \text{fish length at age.}$$

With the Hewitt and Hoenig method, life span or longevity is used to generate a single point estimate, and it is an improvement to the original equation of Hoenig (1983). The newer Charnov method, which incorporates growth parameters, is an improvement to the empirical equation of Gislason et al. (2010) and is based on evidence that indicates that M decreases as a power function of body size. The Charnov method generates age-specific rates of M and is currently in use in Southeast Data Assessment and Review (SEDAR) stock assessments (Williams[6]).

Results

Age determination

A total of 6419 first dorsal spines of gray triggerfish were sectioned. The distribution of samples by area and fishery sector is shown in Table 1. The majority of samples came from the commercial sector in North Caro-

[5] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

[6] Williams, E. 2013. Personal commun. Southeast Fisheries Science Center, National Marine Fisheries Service, Beaufort, NC 28516-9722.

Table 1

Number of samples of first dorsal spines that were available for our age and growth study of gray triggerfish (Balistes capriscus) collected during 1990–2012, primarily from fisheries landings along the coast of the southeastern United States. Five samples were collected during fishery-independent trap sampling off Florida's east coast. Values in the columns for the recreational sector include samples from both the headboat component and the component that includes private recreational boats and charter boats. Samples were collected in the following states: Florida (FL), Georgia (GA), North Carolina (NC), and South Carolina (SC).

	Commercial			Recreational		
Year	FL–GA	NC	SC	FL–GA	NC	SC
1990				18		
1991				5	33	4
1994				1		
1997				2		
2001				2		
2002	8			5		
2003				43		
2004	3	188		60		
2005		386		157	1	
2006		327	140	91	7	13
2007		493	203	17	36	26
2008		676	88	6	13	15
2009		648	92	5	6	21
2010		695	297	1	69	28
2011		1052	220	3	36	23
2012	5					

lina and South Carolina. Approximately 10% of aging samples were from Florida, and the majority of those samples were from the headboat component catches of the recreational sector. Translucent zones were counted on 6267 (97.7%) of the 6419 sectioned spines. Sections from the other 152 spines (2.3%) were determined to be unreadable and were excluded from this study.

For our analysis of increment periodicity, we assigned an edge type to all 6267 samples. Translucent zones were present on the spine marginal edge in all months (Fig. 1); the highest percentage of gray triggerfish with translucent zones occurred from March to June and the lowest from September to February; peak formation occurred in April and May (Fig. 1A). A clear pattern of the width of the opaque margin was noted (Fig. 1B). The narrowest opaque margins (e.g., edge type 2) occurred during June–September, which follows the period of peak formation of the translucent zone. The widest opaque margins occurred during December–March, when the translucent zones start forming again. We concluded that translucent zones on gray triggerfish spines were annuli. Chronological ages resulting from edge analysis were assigned as follows: for fish that were caught from January to June and had an edge type of 3 or 4, the chronological age was the annuli count increased by one; for fish that were caught during the same period and had an edge type of 1 or 2, the chronological age was equivalent to the annuli count; and, for fish that were caught from July to December, the chronological age was equivalent to the annuli count.

Growth increments of gray triggerfish were moderately difficult to interpret. Based on Campana's (2001) acceptable values of APE (5%), agreement was moderate across all 3 readers (MLB–JCP APE=11%, n=198; MLB–MC APE=9%, n=100; JCP–MC APE=12%, n=100; overall APE=11%). Percent agreement values between the 2 primary readers (MLB and JCP) were low (34%) but increased for estimates within (±) 1 year (67%) and within (±) 2 years (86%). An age bias plot indicates that the second primary reader, in comparison with the first primary reader, underestimated gray triggerfish ages, starting at age 5 (Fig. 2), but also shows that the average difference between readers for ages 5–10 was only 1.2 years. These results indicate acceptable between-reader agreement; hence, we included ages from all 3 readers in further analyses.

Growth

Gray triggerfish in this study (n=6267) ranged in size from 173 to 567 mm FL and in age from 0 to 15 years. A single age-0 fish was captured by fishery-indepen-

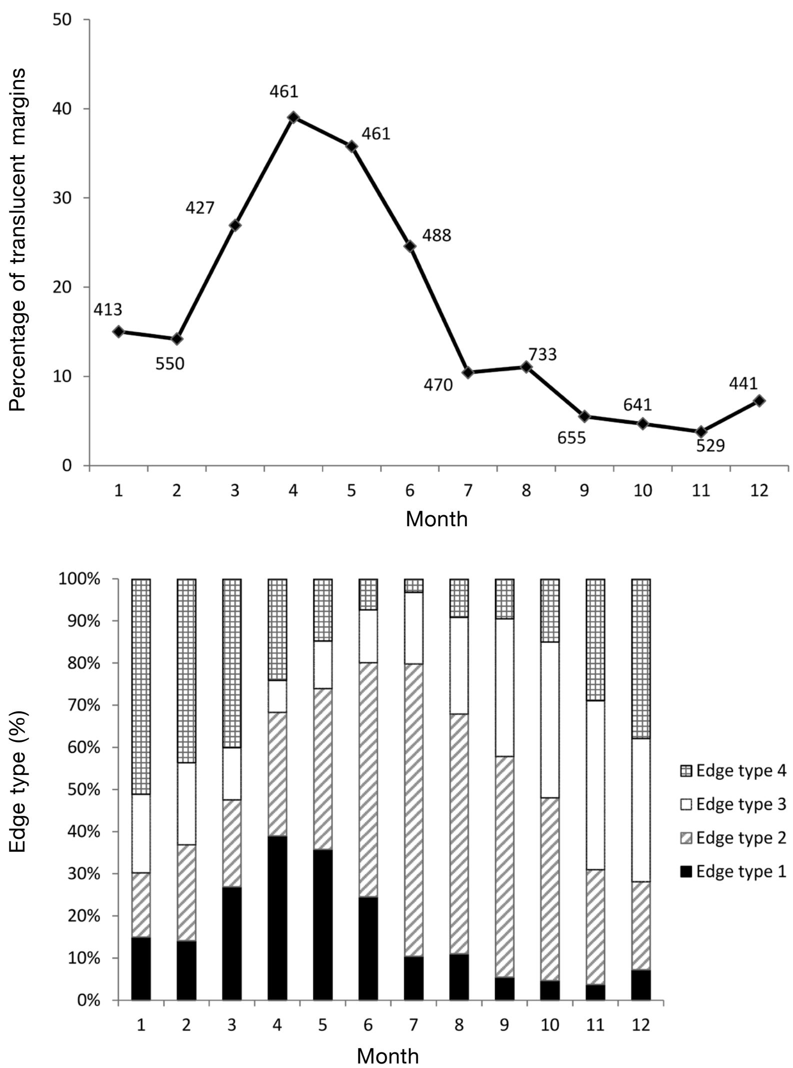

Figure 1

Monthly percentages of (**A**) spine sections with translucent margins on their edges, with monthly sample sizes, and (**B**) monthly percentages of all edge types for gray triggerfish (*Balistes capriscus*) collected from the southeastern United States in 1990–2012. Edge codes: 1=translucent zone on edge, indicating annulus formation; 2=small opaque zone, <30% of previous increment; 3=moderate opaque, 30–60% of previous increment; 4=wide opaque, >60% of previous increment.

dent trap gear, but there were only 13 fish older than age 11 (Table 2). Length and age distributions of the samples by sector (commercial versus recreational) are shown in Figure 3. Visual examination of size and age frequency plots showed no apparent differences in both distributions by sector, with the exceptions that no fish older than age 9 occurred in the recreational samples and commercial samples had fish up to age 15 (Fig. 3A). Modal lengths were 350 mm FL for the commercial sector and 325 mm FL for the recreational sector (Fig. 3B). Mean fork lengths of the specimens by fishery were significantly different: 383 mm FL (standard error [SE] 0.7) for the commercial sector versus 350 mm FL (SE 1.9) for the recreational fishery (t=16.72; df=6253; P=0.0001). The modal age frequency for both fisheries was 4 years (Fig. 3A). Mean ages were found to be significantly different between fisheries: 4.6 years (SE 0.02) versus 4.0 years (SE 0.04) for commercial and recreational sectors, respectively (t=11.9; df=1042.3; P=0.0001).

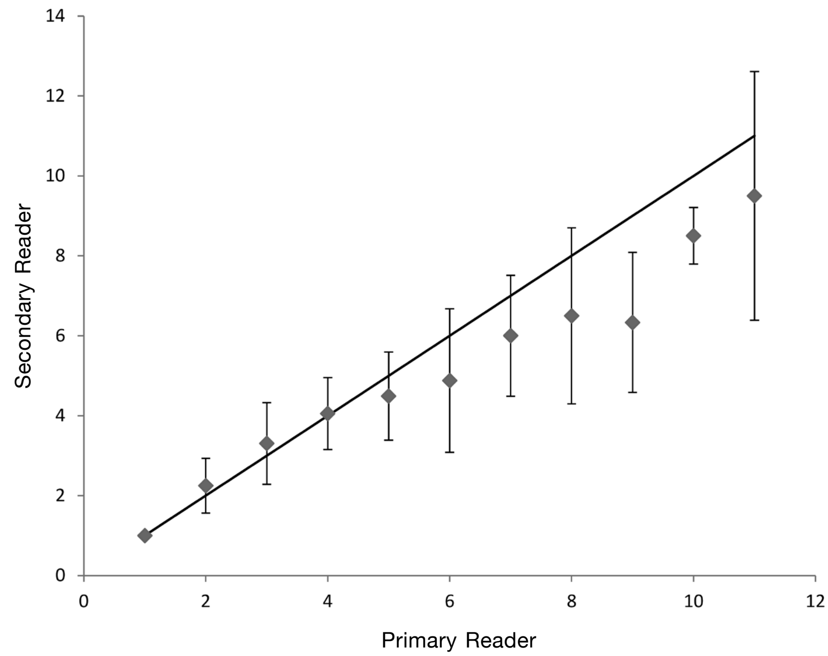

Figure 2

Age bias plot for 198 gray triggerfish (*Balistes capriscus*) sampled from the southeastern United States during 1990–2012 and aged by 2 primary readers. The first reader's mean age estimates are plotted against the second reader's age estimates. Error bars indicate standard deviations.

An ANCOVA of length at age for individual ages revealed no significant differences in size at age between the 2 sectors (P=0.33) for 7 of the 9 ages for which comparisons could be made (Table 3). When the ANCOVA was performed for state, 9 of 11 tests were nonsignificant. On the basis of these results, we pooled data across sectors and states. The resulting von Bertalanffy growth equation was

$$L_t = 457(1-e^{-0.33(t + 1.58)}) \quad (4)$$

for all sectors, states, and sexes combined (n=6267) (Table 4; Fig. 4).

Weight–length relationships

Statistical analyses revealed an additive error term (variance not increasing with size) in the residuals of the W–TL relationship, indicating that a direct nonlinear fit was appropriate. This relationship is described by the following regression:

$$W = 3.1 \times 10^{-5}\, TL^{2.88}\ (n=7618). \quad (5)$$

Residuals of the W–FL relationship exhibited multiplicative error, indicating that a linearized ln-transform fit of the data was appropriate. This relationship is described by the following regression:

$$\ln(W) = 2.98\ \ln(FL) - 17.5,\ (n=20{,}431;\ r^2=0.86) \quad (6)$$

where r^2 is the coefficient of determination. This equation was transformed back to the form

$$W = a \times FL^b \quad (7)$$

after adjustment of the intercept for log-transformation bias with the addition of one-half of the mean square error (MSE) (Beauchamp and Olson, 1973), resulting in this relationship:

$$W = 2.55 \times 10^{-5}\, FL^{2.98}\ (n=20{,}431;\ \text{MSE}=0.035). \quad (8)$$

The relationship between FL and TL is described by the following equation:

$$FL = 30.33 + 0.79 \times TL\ (n=8065;\ r^2=0.84). \quad (9)$$

Natural mortality

Hewitt and Hoenig's (2005) method, which uses maximum age or life span (15 years in this study), estimated that M was 0.28. The method of Charnov et al. (2013), which produces age-specific estimates of M with the use of von Bertalanffy growth parameters, resulted in estimates of 0.65 for age-1 fish, 0.38 for age-5 fish, 0.34 for age-10 fish, and 0.33 for age-15 fish (Table 2).

Table 2

Observed and predicted mean fork length (FL), measured in millimeters, and natural mortality at age (M) data for gray triggerfish (*Balistes capriscus*) collected in 1990–2012 along the coast of the southeastern United States. Standard errors of the means (SE) are provided in parentheses.

Age	n	Mean FL (SE)	FL range	Predicted FL	M
0	1	173	–	181	0.94
1	23	305 (11)	201–394	257	0.65
2	451	333 (2)	214–560	312	0.52
3	1470	353 (1)	190–530	351	0.45
4	1773	375 (1)	229–550	380	0.41
5	1336	391 (1)	221–526	481	0.38
6	684	411 (2)	300–546	417	0.36
7	313	428 (3)	295–543	428	0.36
8	130	444 (4)	330–567	436	0.35
9	53	468 (6)	330–546	442	0.34
10	22	464 (11)	360–550	446	0.34
11	6	416 (30)	323–513	449	0.34
12	4	482 (23)	417–520	451	0.34
13	1	410	–	453	0.33
14	1	496	–	454	0.33
15	1	467	–	455	0.33

Total mortality

Gray triggerfish were fully recruited to the headboat fishery by age 4, to the private recreational fishery by ages 4–5, and to the commercial fishery by age 5. Estimates of Z were similar among all 3 of these sectors. Mean annual estimates of Z for the years 1986–2011 (from all available data) were 0.94 for the headboat fishery and 0.89 for the other recreational fishery. Mean annual total mortality for the commercial fishery was 0.91 for available data (1995–2011, except for 1997 and 2002). Through the use of a pooled catch-at-age matrix across all sectors, Z was estimated at 0.95 (n=15; standard deviation=0.02; range=0.93–0.97). These results equate to an average annual mortality rate of 0.61 across all 3 sectors. Ricker (1975) defined the annual mortality rate A as "the number of fish which die during a year (or season) divided by the initial population number."

Discussion

Gray triggerfish are admittedly difficult to age. First, the use of an external bony structure, the first dorsal spine, to age the fish has some inherent problems, such as possible resorption of the material or damage to the structure—both of which would not likely affect otoliths. Second, the interpretation of the increments on the spines was variable, for reasons such as the spacing between increments and the subjectivity of the presence of false annuli. Because of these problems, we, along with members of the staff of another laboratory that has been involved in aging fishery-independent samples of gray triggerfish, held a workshop to address issues with aging this fish. A robust set of criteria for interpreting the increments on the spine was established during this workshop. Using these newly established criteria, we reread a set of their samples. We found consistent agreement between readers and within readers in our own study, as evidenced by the APE calculations presented in the previous section. Therefore, the results of this study represent the best available information on the longevity and growth of gray triggerfish.

The spine edge analysis conducted in this study strongly indicates that gray triggerfish deposit one annulus per year from March to June and that peak annulus formation occurs in April and May. This result is similar to findings in other studies where peak annulus formation occurred in June and July in gray triggerfish in the Gulf of Mexico (Johnson and Saloman, 1984) and in June in fish from the east coast of the United States (Moore, 2001) (Table 4). The timing of the deposition of a growth increment in Moore's study was concurrent with peak spawning in June and July. Gray triggerfish in the Gulf of Mexico also have exhibited temporally similar times of annulus formation and peak spawning (Simmons and Szedlmayer, 2012).

Weight–length relationships were nearly identical for gray triggerfish from the SEUS and the Gulf of Mexico. The relationship between FL and TL was also similar: $FL=30.33+0.79\times TL$ for fish off the Atlantic

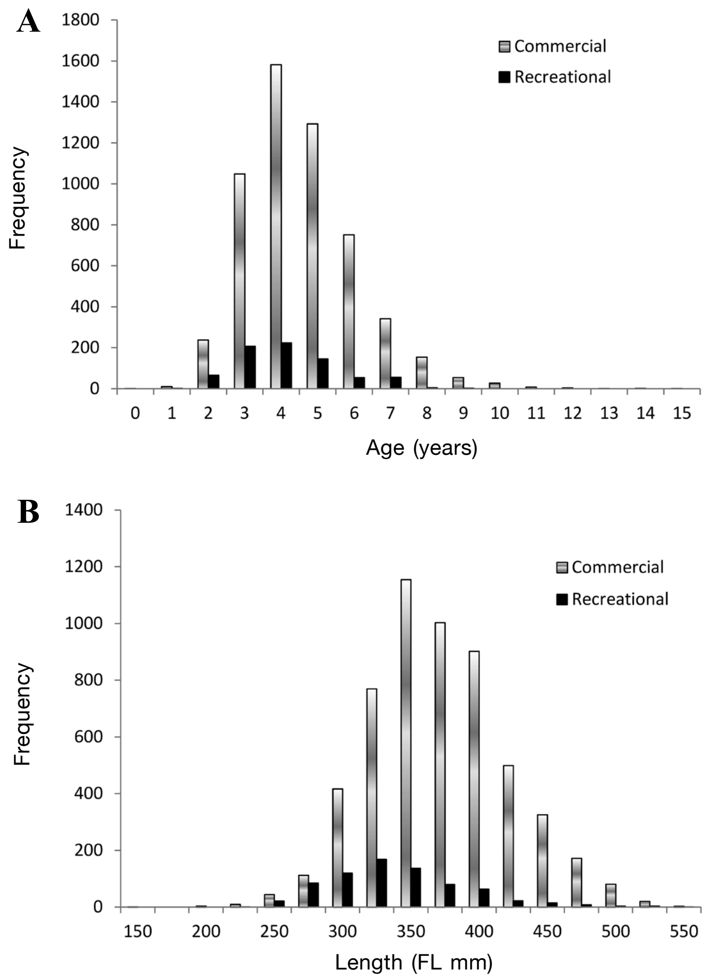

Figure 3

Distributions of (**A**) age frequency and (**B**) length frequency, by fishing sector, for aging samples of gray triggerfish (*Balistes capriscus*) collected from the southeastern United States in 1990–2012.

coast versus FL=29.70+0.77×L for the Gulf population (Johnson and Saloman, 1984).

Gray triggerfish grew moderately fast, attaining an average observed size of 353 mm FL (14 in) by age 3 (Table 2). This result compares favorably with the finding of Johnson and Saloman (1984) that gray triggerfish from the Gulf of Mexico also grow moderately fast at earlier ages, attaining an average size of 357 mm FL by age 3, growing an average of an additional 50 mm per year through age 5, and averaging gains in growth of 15 mm per year at ages 6–13. Growth of fish in our study slowed after age 3, reaching 496 mm FL by age 5, and then averaging annual size increment increases of 21 mm through age 10.

Several previous studies have found that male gray triggerfish are substantially larger than female fish (Johnson and Saloman, 1984; Moore, 2001; Simmons and Szedlmayer, 2012). These findings justify the generation of sex-specific growth curves if possible. Unfortunately, the specimens we used were collected under sampling protocols that did not allow for the collection of sex-specific data. We recommend that strategies to obtain these data would be beneficial in future studies, if possible.

Because our aging structures came from specimens acquired exclusively from fishery-dependent sources and, therefore, may be more representative of the fished population than the whole population, we advise caution in interpretation of gray triggerfish growth curves, especially for the region of the curve that describes the youngest ages. Minimum size regulations could have an effect on the size of fish available to

Table 3

Results of analysis of covariance of length at age testing for differences by fishery (recreational and commercial) and state (NC, SC, FL–GA) between gray triggerfish (*Balistes capriscus*) aging samples collected during 1990–2012. An asterisk (*) indicates a significant probability value. A dash indicates that the sample distribution did not allow for a test of significance.

Age	n	Fishery	State	Fishery*State
0	1	–	–	–
1	23	F=0.03, P=0.87	F=5.76, P=0.02*	–
2	451	F=2.01, P=0.157	F=1.59, P=0.20	F=7.02, P=0.001*
3	1470	F=16.74, P=0.001*	F=0.94, P=0.39	F=1.27, P=0.28
4	1773	F=0.33, P=0.56	F=1.46, P=0.23	F=0.83, P=0.43
5	1333	F=0.23, P=0.63	F=0.81, P=0.44	F=2.76, P=0.06
6	684	F=2.27, P=0.13	F=0.001, P=0.99	F=2.80, P=0.06
7	313	F=4.58, P=0.03*	F=2.06, P=0.12	F=1.09, P=0.33
8	130	F=2093, P=0.09	F=0.63, P=0.53	F=0.03, P=0.43
9	53	F=1.82, P=0.18	F=10.75, P=0.0001*	–
10	22	–	F=0.14, P=0.71	–
11	8	–	F=1.08, P=0.34	–
12	4	–	–	–
13	1	–	–	–
14	2	–	–	–
15	1	–	–	–

generate growth estimates. Even though size limits existed only for fish taken from waters off the eastern coast of Florida during our study (432 of 6267 fish, or 7%), we re-ran the growth model using the method of McGarvey and Fowler (2002), which adjusts for the bias imposed by minimum size limits, and we found no effect of minimum size limits on our parameter estimates. We are confident that our samples represent the smallest fish recruited to the hook-and-line gears. Nevertheless, we collected few fish younger than age 2. It is probable that more comprehensive sampling with fishery-independent gear would capture younger gray triggerfish.

As another strategy to address the lack of smaller, younger fish and the effect this deficiency may have on estimation of the early part of the growth curve,

Table 4

Comparison of life history parameters of gray triggerfish (*Balistes capriscus*) from various studies. L_∞=asymptotic length; K=growth coefficient; t_0=theoretical age at length of zero; SEUS=southeastern United States; and FL=fork length.

	Parameter					
Study	L_∞ (mm)	K	t_0	Peak in translucent edges	Peak spawning	Maximum age (yr)
Johnson and Saloman (1984)—U.S. Gulf of Mexico	466 FL	0.38	– 0.19	June–July	April–May	13
Moore (2001)—SEUS						
Males	521 FL	0.17	–2.03	June	June–July	10
Females	443 FL	0.19	–2.26	June	May–Sept	9
Escorriola (1991)	571 FL	0.19	–0.15	July–Sept	–	13
Burton et al. (current study)	457 FL	0.33	–1.58	April–May	–	15

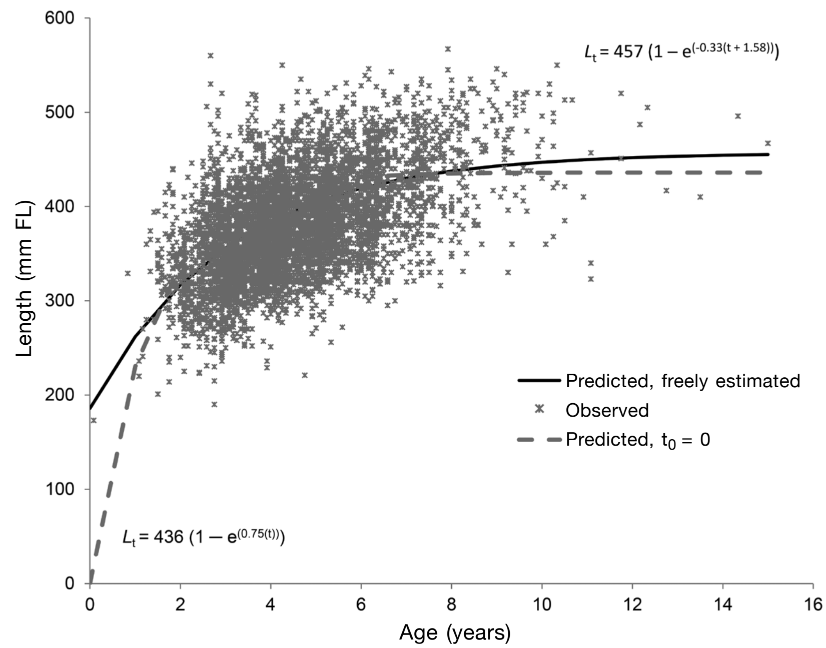

Figure 4

Observed and predicted lengths at age, measured in fork lengths (FLs), for gray triggerfish (*Balistes capriscus*) sampled from the southeastern United States in 1990–2012. L_t=length at age t; t_0=theoretical age when length equals zero.

we recommend estimating growth parameters with a fixed t_0 value, such as −0.5 (Burton et al., 2012) or zero (Burton et al., 2014). This method has the effect of pulling the growth curve down to simulate smaller length at age for fish at the youngest ages. We re-estimated growth parameters of gray triggerfish with a fixed value of t_0=0. The value of the growth coefficient K increased measurably (0.75 versus 0.33, when freely estimated) because of the steepness of the initial part of the curve (Fig. 4). The theoretical maximum length L_∞ decreased marginally, 436 mm FL versus a freely estimated value of 457 mm FL. This result is not unexpected because L_∞ and K are negatively correlated with each other (Ricker, 1975; Xiao, 1994). The 2 growth curves are very similar from age 2 on, with only minor differences in size at age at the oldest ages.

Our theoretical growth curve fitted the observed data well (Fig. 4). Growth parameters estimated in our study compare very closely with the study of gray triggerfish in the Gulf of Mexico (Johnson and Saloman, 1984), and it is interesting to note that fish samples came primarily from fishery-dependent sources in both studies. In Moore's (2001) study, samples were obtained from both fishery-dependent and fishery-independent sources and yielded markedly different growth parameters between male and female gray triggerfish, but no differences in growth parameters estimates were found between the fishery-dependent and fishery-independent data sets.

Natural mortality of wild populations of fishes is difficult to measure. A single estimate of M for the entire life span of a fish is unreasonable, except for fish that have attained a maximal size that renders them invulnerable to large-scale predation. The Hewitt and Hoenig (2005) estimate of M is based on the maximum age a species can attain in an unfished population. In this sense, the point estimate of M, derived with Hewitt and Hoenig's (2005) method, can serve as a lower boundary for the estimate of M derived for older ages by an age-varying method. The maximum observed age from our study was 15—a result that compares favorably with the maximum age of 13 found by Escorriola (1991) and Johnson and Saloman (1984). We feel this age is a realistic maximum age for gray triggerfish because no other study has found an older age, including studies that might be considered more representative of the population at large because they included fishery-independent samples as well (Moore, 2001). We think our estimates are reasonable given that our age-specific estimate of M=0.33 for the older ages that was derived by using the method of Charnov et al. (2013) compares closely with the point estimate of M=0.28 found with the method of Hewitt and Hoenig (2005) (Table 2).

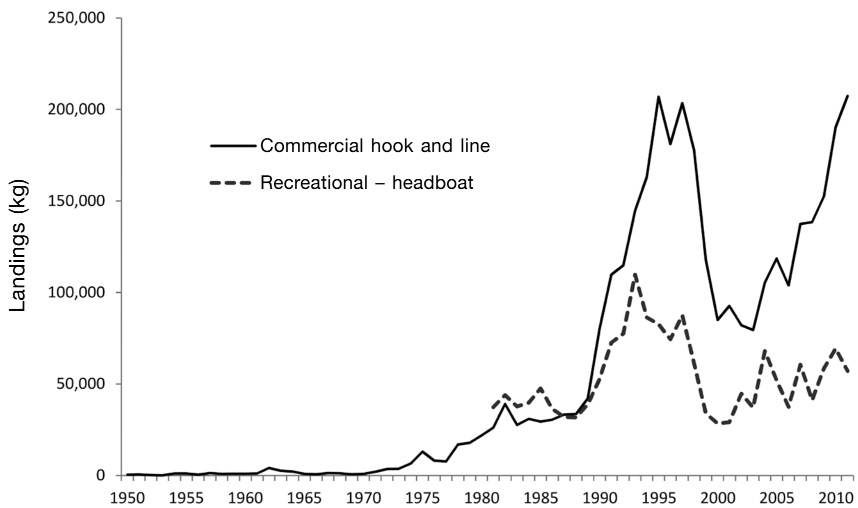

Figure 5

Historical landings of gray triggerfish (*Balistes capriscus*) for the hook and line fishery of the commercial sector and the headboat component of the recreational sector in the southeastern United States in 1950–2012.

Our estimates of Z from catch curve analysis are substantially higher than the values found by Johnson and Saloman (1984) for gray triggerfish in the Gulf of Mexico. The average annual estimate of Z was 0.95 across all sectors pooled, compared with Johnson and Saloman's (1984) estimates of 0.40–0.69, depending on the method used. Whereas they found that recruitment to the hook-and-line gear occurred at age 3, results from our study indicate that full recruitment occurred at age 4 or 5. These observations compare with Moore's (2001) finding of no fishery-dependent samples younger than age 3.

A benchmark stock assessment of gray triggerfish in the SEUS is unavailable, although one is currently underway. A report on trends of static spawning potential ratios estimated for 15 species of reef fishes showed that mean weights for gray triggerfish decreased by an average of 50% in both the recreational and commercial sectors in 1983–99, and catch per unit of effort (CPUE) for the headboat sector increased eightfold during 1989–97 before declining (Potts and Brennan[7]). This drop in CPUE in 1997 coincides with the enactment of the 305-mm minimum size limit in Florida waters; however, we doubt that the regulation caused the drop in CPUE because a small percentage of overall gray triggerfish landings come from waters in Florida.

Both the commercial sector and the headboat fishery of the recreational sector showed marked increases in magnitude of landings around the period from 1989 to 1996 (Fig. 5). Landings leveled off in 2000 for both fisheries but increased again in 2002. We interpret increased landings through the 1990s as an increased desirability by the public for gray triggerfish as a food fish. Before this time, gray triggerfish were mostly discarded by anglers or commercial fishermen because they were perceived as trash fish and unmarketable. Figure 5 shows that the perception of this species as undesirable changed considerably beginning in 1990. Fishermen, especially commercial fishermen, began keeping gray triggerfish when a viable market developed for them. As new regulations limited the harvest of other, more desirable species, fishermen began to target gray triggerfish. The dramatic increase in landings (as well as decreases in mean weight in all fisheries), increases in CPUE in the headboat fishery, and fairly high estimates of total mortality all indicate that gray triggerfish populations in the offshore waters of the SEUS need to be rigorously assessed in terms of stock health and overfishing status.

This study has shown that spine sections in gray triggerfish are reliable structures for aging. The data from this study of gray triggerfish in the SEUS indicate that growth rings are laid down once a year in the spring months and that growth is moderately fast for the first 5 years of life. Estimates of M are reasonable for a fish with moderate life spans (maximum age of 15 years). Estimates of Z are relatively high in the commercial sector and in both components of the rec-

[7] Potts, J. C., and K. Brennan. 2001. Trends in catch data and estimated static SPR values for fifteen species of reef fish landed along the southeastern United States, SEDAR4-DW-28, 41 p. [Available from http://www.sefsc.noaa.gov/sedar/.]

reational sector and are likely a result of the increasing exploitation of this species that is exacerbated by increases in desirability and in marketability to consumers. We believe the results of this study accurately describe the fished population of gray triggerfish in the offshore waters of the SEUS. A NMFS stock assessment is currently underway as of this writing, and we feel the data provided in this study will be a valuable contribution to these efforts.

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