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Age and growth of grey triggerfish *Balistes capriscus* from trans-Atlantic populations

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Abstract

Anthropogenic factors that negatively impact reef fishes can include changes in life-history patterns of fisheries-targeted species. Understanding these impacts on growth and population age structure is essential in the management of exploited populations of fishes. This is the first study to directly compare age and growth for a major fisheries species between east and west populations of a transatlantic reef fish. The main goal of this study was to document age and growth in grey triggerfish *Balistes capriscus* from coastal waters of Ghana in the Gulf of Guinea (GOG) and compare those with the previous growth studies from that region and with the western Atlantic population. A secondary objective of this study was to evaluate the use of otoliths to age triggerfish and to provide a preliminary comparison with spine-derived age estimates. The results obtained from this study provided an updated understanding of the growth and age structure of the eastern *B. capriscus* population in GOG. The authors documented that shifts in population attributes occurred for *B. capriscus* after its major decline in abundance. The differences in physical and biotic characteristics of the East and West Atlantic regions and the differences in collection methods of samples make direct comparisons of growth parameters difficult. Nonetheless, overall differences in maximum sizes and ages were apparent; the western Atlantic population had a larger maximum size and older maximum age. The authors also documented that sagittal otoliths can be used to provide age estimates for triggerfish species, and otoliths as an ageing structure had better between-reader precision compared to dorsal spines.

KEYWORDS
Gulf of Guinea, reef fish, triggerfish otoliths

1 | INTRODUCTION

Across the oceans, reef fishes are impacted by anthropogenic factors such as intense fishing pressure (Dulvy *et al.*, 2003; Friedlander & DeMartini, 2002; Hughes, 1994; Paine *et al.*, 1998), habitat alteration and loss (Alvarez-Filip *et al.*, 2015; Darling *et al.*, 2017; Holbrook *et al.*, 2015), and the introduction of nonnative species (Albins, 2015; Benkwitt, 2015; Johnston & Purkis, 2016). Several studies have noted that these stresses can result in changes in life-history patterns of fisheries-targeted species (Ali *et al.*, 2003; Coleman *et al.*, 2004;
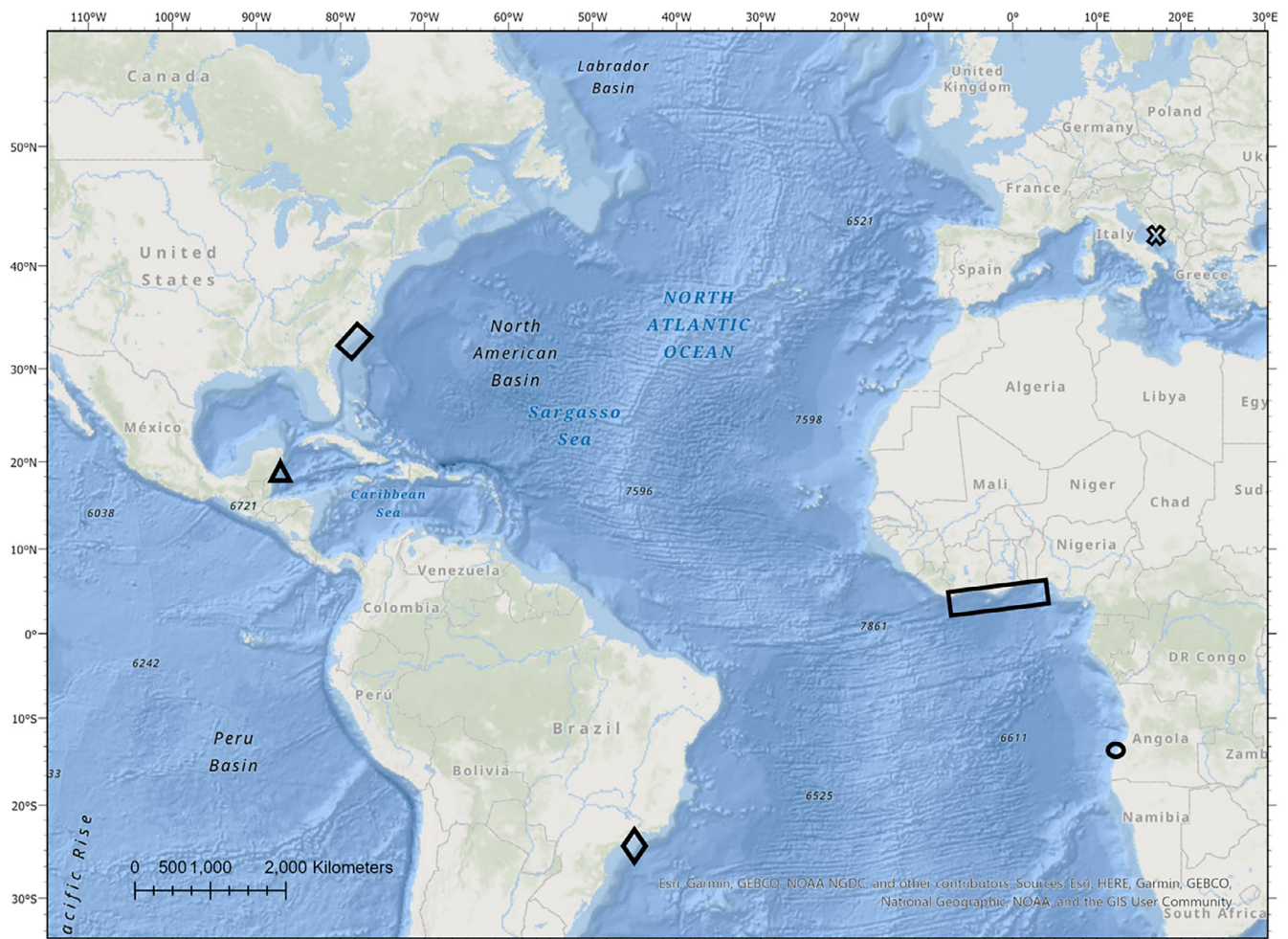
Lorenzen & Enberg, 2002). Understanding how these stressors impact growth and population age structure is essential in the management of exploited populations of fishes (Ali *et al.*, 2003; Lorenzen & Enberg, 2002).

Species in the triggerfish family Balistidae support productive fisheries across the globe, north and south of the equator in regions throughout the Atlantic and Pacific Oceans (Aggrey-Fynn & Sackey-Mensah, 2012; Barroso-Soto *et al.*, 2007; Bernardes, 2002; Ferreira de Menezes, 1979; Kacem & Neifar, 2014; Matos-Caraballo, 2012). The species grey triggerfish *Balistes capriscus* Gmelin, 1789 supports

fisheries in the eastern and western Atlantic Ocean (Aggrey-Fynn, 2013; Johnson & Saloman, 1984; Kacem & Neifar, 2014; Kelly-Stormer *et al.*, 2017), and its biology and ecology have been investigated throughout most of its range. In waters of the Gulf of Mexico (GOM) and southeastern coast of the United States (SEUS), *B. capriscus* is moderately long-lived (maximum reported age of 15 years; Johnson & Saloman, 1984) and reaches a reported maximum size of 697 mm fork length (Allman *et al.*, 2018). Western Atlantic *B. capriscus* spend their early juvenile stage in the water column, associated with floating mats of sargassum (Casazza & Ross, 2008; Ingram, 2001; Wells & Rooker, 2004), and then settle into and remain as adults in benthic habitats characterized by hard-bottom and a range of complex structure including rocky outcroppings and natural low-to-moderate profile reefs of corals and sponges across the SEUS and GOM shelf (Miller & Richards, 1980; Muhling *et al.*, 2014; Sedberry *et al.*, 2006). Adult *B. capriscus* in the western Atlantic feed diurnally mainly on benthic invertebrates associated with reefs, including

molluscs, crustaceans and echinoderms (Blitch, 2000; Frazer *et al.*, 1991; Vose & Nelson, 1994). They will also forage for other invertebrate prey in nearby sandy areas, consuming species of sand dollars and sea urchins. Fishing pressure on *B. capriscus* in U.S. waters is relatively high; in the SEUS, it is one of the top 10 reef species fished in terms of average annual landings (Burton *et al.*, 2015).

In the eastern Atlantic, less is known about the biology and ecology of *B. capriscus* along the coast of Africa in the western Gulf of Guinea (GOG). No studies in the peer-reviewed literature have reported on ontogenetic shifts from pelagic to benthic habitats in that region, and only trawling surveys have been used to investigate *B. capriscus* habitat preferences and abundance (Koranteng, 1998). *B capriscus* in GOG is targeted mainly as part of artisanal and inshore fisheries using bottom trawls, purse seines and hook-and-line gear within shelf waters from Senegal to Nigeria (Figure 1). One study on the age and growth of *B. capriscus* (Table 1) sampled fish in 1980 and reported a maximum age of *c.* 4 years and size of 340 mm FL

FIGURE 1 Northern and southern portions of the Atlantic Ocean where *Balistes capriscus* occurs. The rectangles in the West and East Atlantic denote areas sampled for the current study. The circle indicates the most southern extent of the eastern Atlantic range of *B. capriscus*. The diamond indicates the location of the fish sampled from Brazil waters. The X indicates the most northern location in the eastern Atlantic where *B. capriscus* have been studied. The triangle (Δ) denotes the reported location of spawning aggregation of *B. capriscus* studied off the Yucatán Peninsula in the tropical western Atlantic

TABLE 1 Summary of grey triggerfish age and growth research from the East Atlantic in the Gulf of Guinea

	n	Size mean/mode Size range(mm L_F)	Age mean/mode Age range(year)	L_∞	K	t_0
1980	55 (568)	211/190 140–310 Max size = 340	1.9/2 1–4	E-F: 408 Obs: 352	E-F: 0.43 Obs: 0.47	E-F: 0 Obs: −0.18
2005	66 (84)	NA/275 (123–362) Max size = 449	5.6/6 1–11	392	0.21	−0.29
2012–2014	115 (115)	283/276 166–371	4.4/4 1–9	334	0.47	−0.20

Note: Results for 1980 samples were reported in Ofori-Danson (1989) and for 2005 samples in Aggrey-Fynn (2009). In the original 1980 study, an "eye-fitted" (E-F) curve was used to obtain von Bertalanffy growth parameters. Using the original observed size-at-age data from that study, the growth parameters (Obs) were recalculated using the same methods described for the current data. NA, not available. In the first column, *n* is the number of samples collected that were aged, and the values in parentheses are the total number of samples collected and measured for length in that study.

(Ofori-Danson, 1989). A second study sampled *B. capriscus* in 2005 and reported a maximum age and size of 11 years and 449 mm FL, respectively (Aggrey-Fynn, 2009).

Quantitative assessments of fishery stocks can benefit from documentation of growth rates and growth rate change over time, because it is an important compensatory response of fish populations to fishing pressure (Ali *et al.*, 2003; Coleman *et al.*, 2004; Lorenzen & Enberg, 2002). The determination of a fish population's age structure and growth parameters is dependent on accurate and precise estimates of age, and therefore the impacts of age estimate uncertainty or bias can ultimately impact evaluation of other population metrics including estimates of survival, mortality and biomass (Allman *et al.*, 2018; Anderson *et al.*, 2008; Gamboa-Salazar *et al.*, 2020; Pardo *et al.*, 2013). *B. capriscus* has been aged using the first dorsal spine for over 30 years. The main reason for this seems to be that the dorsal spine is an easy structure to obtain relative to triggerfish otoliths that are small, fragile and difficult to extract (Aggrey-Fynn, 2007; Hood & Johnson, 1997). Hood and Johnson (1997) justified their use of the dorsal spine with the following statement: "we chose dorsal spines as aging structures for gray triggerfish because they were easier to remove than otoliths." Nonetheless, otoliths have several properties that set them apart from all other skeletal structures and support their use in accurately estimating age and growth in fishes (Campana, 2001). Research comparing the precision and accuracy of age estimates from external ageing structures in fishes to otolith-based age estimates shows that those structures, including spines, fin rays and scales, can significantly underestimate the true age of a fish (Buckmeier *et al.*, 2002; Buckmeier *et al.*, 2012; Gu *et al.*, 2013; Lozano *et al.*, 2014). In addition, the age studies of *B. capriscus* that include a measure of precision in spine age estimates consistently report low precision for the structure. Otoliths have not been used for estimating age in triggerfish species.

The main goal of this study was to document age and growth in *B. capriscus* from coastal waters of Ghana in the GOG and compare those with the previous growth studies from that research and with the western Atlantic population. A secondary goal of this study was to

evaluate the use of otoliths to age *B. capriscus*. Specific objectives were as follows: (a) document age and growth for *B. capriscus* from Ghana and compare the findings with previous assessments from 2005 (Aggrey-Fynn, 2009) and 1980 (Ofori-Danson, 1989); (b) compare the eastern Atlantic population with age and growth of a western Atlantic population that ranges from offshore North Carolina (NC) and South Carolina (SC), using samples from fisheries-dependent and -independent sources; and (c) provide a preliminary evaluation of using otoliths as an ageing structure for triggerfish species.

2 | MATERIALS AND METHODS

2.1 | Ethics statement

Fish samples obtained by the authors of this study and reported on here were collected and handled in strict accordance within the guidelines of the *U.S. Government Principles for the Utilization and Care of Vertebrate Animals Used in Testing, Research and Training* (https://olaw. nih.gov/sites/default/files/PHSPolicyLabAnimals.pdf). This research was conducted under USCA IACUC protocol #053012-BIO-04.

2.2 | Study regions

Triggerfish samples for the eastern Atlantic triggerfish GOG population were obtained from coastal waters of Ghana in West Africa (Figure 1). The Ghana coastline extends 536 km in length, stretching from 3° 06′ W to 1° 10′ E and between 4° 30′ and 6° 6′ N with the shelf extending 13 km from shore near the western and eastern borders, up to 80 km in the middle, encompassing a total estimated area of 23,700 km^2 (Koranteng, 2001).

Triggerfish for the western Atlantic were collected from off the coasts of North Carolina and South Carolina, U.S.A., which is characterized by a wide shelf that extends up to 145 km from shore (Figure 1). In this region, grey triggerfish commonly occur in the mid-

shelf (20–30 m depths), outer-shelf (30–50 m depths) and shelf-edge (50–100 m depths) zones (Muhling *et al.*, 2014; Sedberry *et al.*, 1998; Sedberry *et al.*, 2006; Sedberry & Van Dolah, 1984). The mid-shelf and outer-shelf are characterized by several habitat types, including unconsolidated soft bottom, sandy substrate covering hard bottom with anthozoans, sponges, polychaetes, hydroids, bryozoans and ascidians, and emergent hard bottom and rocky outcrops dominated by gorgonian corals and sponges, which provide low-to-moderate profile structural complexity (Wenner, 1971). *B. capriscus* occurs across the shelf habitat types characterized by hard bottom, low-to-moderately high-profile reef structures within a range of optimal bottom temperatures (Muhling *et al.*, 2014).

2.3 | Sample collection

Balistes capriscus were collected from two main regions of the North Atlantic: the portion of the GOG that occurs in coastal waters of Ghana and in the western Atlantic waters of the coasts of North Carolina and South Carolina (NC/SC). Fish samples in Ghana waters (hereafter referred to as East Atlantic) were obtained from local trawlers, purchased directly from fishers in 2012–2014. Fish samples in NC/SC waters are divided into fisheries-dependent and -independent samples. Fisheries-dependent samples (hereafter referred to as West Dependent) were opportunistically collected from fisheries landings in SC during 2012–2014. These fish were caught by commercial and recreational fishers using conventional vertical hook-and-line gear, stored on ice and then filleted upon return to shore. Immediately after filleting, the remaining carcass was frozen until further processing. Fisheries-independent samples were collected with chevron traps from 2011 to 2012 as part of the Southeast Reef Fish Survey (SERFS) from waters of NC/SC. The fisheries-independent (hereafter referred to as West Independent) *B. capriscus* samples used in the current study are a sub-set of samples collected as part of an extensive *B. capriscus* life-history study that included samples from 2009 to 2012 collected from waters of Florida, Georgia, NC/SC (Kelly-Stormer *et al.*, 2017). A detailed description of the sampling protocol and design for the SERFS fisheries-independent research and monitoring efforts with *B. capriscus* and other reef fish species is provided in Kelly-Stormer *et al.* (2017) and Sinkus *et al.* (2019).

All grey triggerfish samples for this study were weighed (when obtained intact) to the nearest gram and measured for standard length (L_S), fork length (L_F) and total length (L_T) to the nearest millimetre. Separate Kolmogorov–Smirnov (K–S) tests were used to make pairwise comparisons to determine if the population size structure of *B. capriscus* differed among the three sample-sources. A one-factor ANOVA was used to determine if significant differences existed in mean size among the three sample-sources with size (L_F) as the dependent variable. Dunnett's T^3 *post hoc* comparisons were made to identify pair-wise differences between sample sources. Statistical analyses were conducted in SPSS (IBM Corp. 2012), and the results were considered significant at *P*-values less than 0.05. If the assumptions for statistical tests were not met, then data were log transformed.
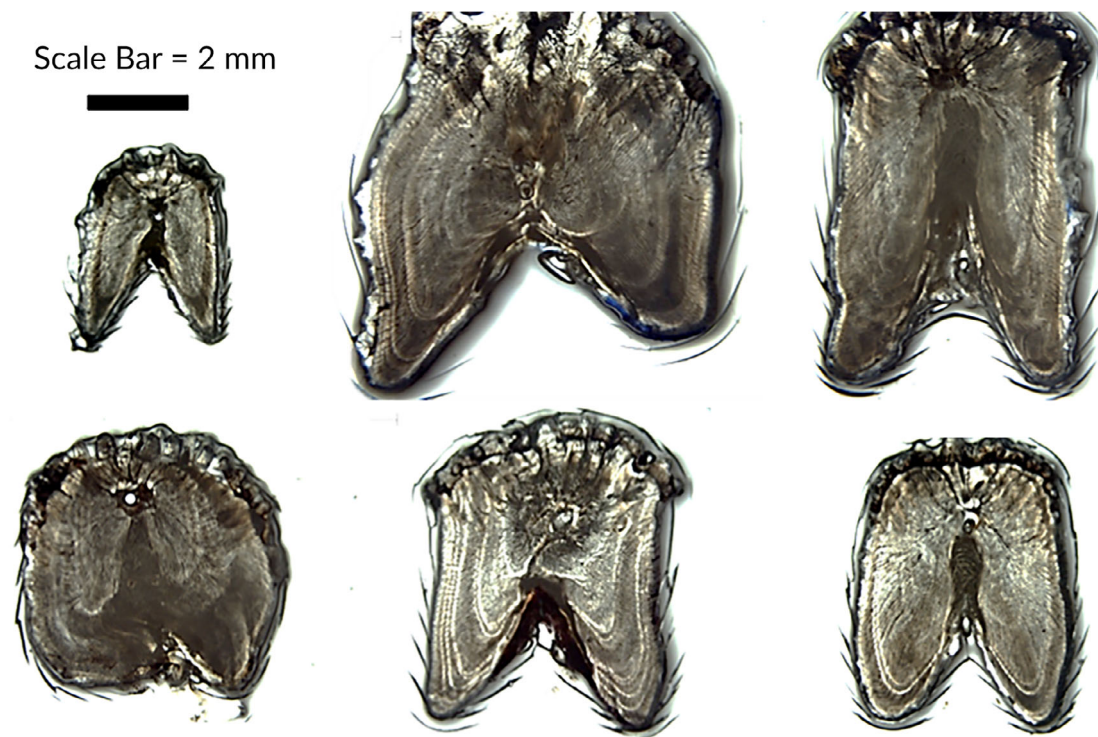
2.4 | Age and growth

The first dorsal spine is currently the accepted structure for estimating age in *B. capriscus* (Kelly-Stormer *et al.*, 2017; Patterson *et al.*, 2019) and was used in previous studies for this species from the eastern and western Atlantic (Burton *et al.*, 2015; Kelly-Stormer *et al.*, 2017; Ofori-Danson, 1989). 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) using a low-speed saw with a diamond-edged blade, then mounted on glass slides with a clear mounting medium and viewed using a dissecting microscope at 10–20× magnification with transmitted light (Figure 2). Increment count was determined by identifying and enumerating the pattern of faster-growing (opaque) and slower-growing (translucent) zones assumed to represent 1 year of peak growth and slow growth seasons, respectively. Fish age was estimated for each spine section by counting the number of translucent zones on the spine section (Figure 3). At least two independent readers evaluated spine increments on a section without knowledge of fish length or date of capture. Increment counts were considered age estimates. 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 (y). Other studies have reported low between-reader precision for *B. capriscus* spine age estimates (Burton *et al.*, 2015; Kelly-Stormer *et al.*, 2017); therefore, the current study used the same method, average per cent error (APE), to assess between-reader precision so that estimates could be compared among studies (Beamish & Fournier, 1981).

The age frequency distributions between *B. capriscus* populations were compared using pair-wise K–S tests. A one-factor ANOVA was used to determine if significant differences existed in mean age among the three sample sources with age as the dependent variable. Dunnett's T^3 *post hoc* comparisons were made to identify pair-wise differences between sample sources. For each of the sample sources (East Atlantic, West Dependent and West Independent), von Bertalanffy growth functions were fit to fractional age data with the least squares method using the solver function in Microsoft Excel (Haddon, 2010). Fractional age data were calculated as described in Kelly-Stormer *et al.* (2017) using peak month of spawning for each region. To provide more representative estimates of growth parameters for each of the sample sources, 12 newly settled juvenile grey triggerfish that were collected from *Sargassum* spp. off the SC coast during 2011–2014 were included in the growth models and processed for age determination (Kelly-Stormer *et al.*, 2017).

2.5 | Comparison between ageing structures

After an initial evaluation of the location of *B. capriscus* and queen triggerfish *Balistes vetula* Linnaeus, 1758, otoliths within the cranium of 25 samples for each species, a method was developed to cut
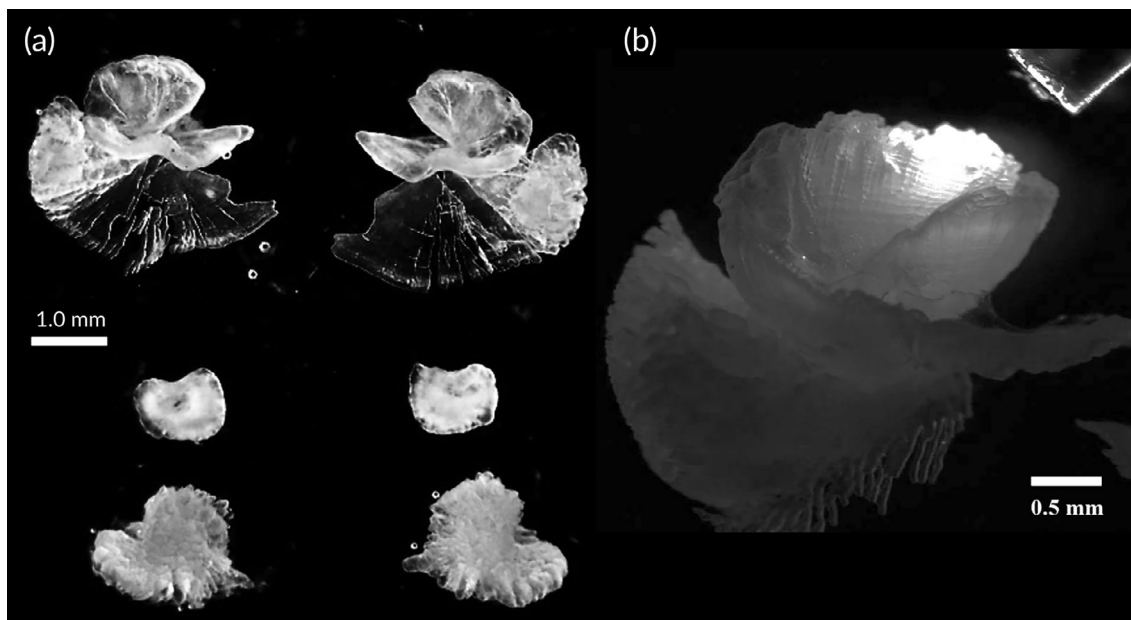
FIGURE 2   Examples of the variety of shapes and forms observed in the first dorsal spine sections of *Balistes capriscus*

FIGURE 3   Examples of a section from the first dorsal spine (a) and a section from the sagittal otolith (b) from a *Balistes capriscus* fish. Circles denote the translucent zones observed on the dorsal spine (increment in spine = 1 opaque zone + 1 translucent zone) and the opaque zones observed on the otolith section (increment in otolith = 1 translucent zone + 1 opaque zone)

through the head *c.* 0.5 cm behind the dorso-anterior edge of the occipital bone that exposed the left and right otic cavities containing the three pairs of otoliths. Thus, the authors were able to easily extract all three otoliths from the left and right sides, still encased in the otolithic membranes. From this, they were able to document the location of each otolith in the context of the inner ear structure and determine which otoliths were the sagittae, lapillae and asteriscae (Figure 4). Once the authors developed this method to extract

FIGURE 4 Examples of *Balistes capriscus* otoliths. (a) The left and right otoliths of the three otolith pairs from a triggerfish (top to bottom: sagitta, astericus and lapillus). (b) Image demonstrating the use of a fibre optic cable to concentrate reflected under a stereoscope when identifying and counting opaque zones on a triggerfish sagittal otolith

triggerfish otoliths with ease, without breaking the delicate sagittal otoliths, they proceeded to collect the otoliths from the West Dependent *B. capriscus* samples.

All three otolith pairs (still encased in the otolithic membranes) were extracted from the samples and placed in label vials for further processing. The authors determined that because of the fragile nature of the sagittal otoliths, it was best to leave them in their protective sacule tissue until each otolith was ready to process. Initially the authors evaluated the best way to obtain increment counts from triggerfish otoliths by reading them in two ways: (a) embedding and sectioning otoliths, and then mounting the sections on slides (Figure 3); and (b) reading the otolith whole, using a combination of reflected light and a fibre optic cable to concentrate the light along the sulcular groove (Figure 4). A total of 20 sagittal otolith pairs were used in this evaluation with one otolith embedded/sectioned and the other read whole. From this comparison, the authors determined that because of the unique shape and small size of triggerfish sagittal otoliths, it was difficult to embed them at a consistent orientation to obtain a readable section; of the 20 sectioned otoliths, only five produced readable sections (Figure 3). Using the fibre optic cable method, the authors were able to visualize clear opaque zones to count (Figure 4); therefore, they proceeded with this method for the rest of the triggerfish otoliths.

When it was time to read a sagittal otolith, the authors carefully removed it from the sacule tissue with the aid of a stereoscope. This provided them with consistent, relatively undamaged whole otoliths to then immediately read. Under the stereoscope at a magnification of 20–40×, otoliths were submerged in water against a black background, and then using the fibre optic cable attached to the light source, the areas along the sulcular groove were illuminated and the each opaque zone present was counted (Figure 4). Otoliths from each fish were read by a primary reader with no knowledge of fish size and date of sample collection. A random sub-set of 100 otoliths was read by a second reader, with no knowledge of fish size, date of collection or increment counts by the first reader. The age estimates from the two readers were compared, and APE was calculated as previously described for spines. When a disagreement occurred, the two readers examined the otolith together and obtained a consensus age estimate to use in further analysis. Each reader had 8+ years of experience in age estimation of fishes. A von Bertalanffy growth function was calculated from otolith age estimates as previously described for spines. A two-factor ANOVA was used to test the effect of ageing structure on estimated size at age for ages 3–6, the most prevalent age classes present in the data. The dependent variable for this was L_F and was ln-transformed to meet parametric assumptions. The independent variables were age class and ageing structure.

3 | RESULTS

3.1 | Fish collection

A total of 115 *B. capriscus* were collected in Ghana waters in the East Atlantic during 2012–2014, ranging in size from 166 to 371 mm FL (Table 1; Figure 5). From 2012 to 2014, a total of 642 West Dependent samples were obtained ranging in size from 231 to 520 mm FL (Table 2; Figure 5). A total of 416 West Independent samples were collected from 2011 to 2012 ranging in size from 155 to 518 mm FL (Table 2; Figure 5). Mean size differed significantly among the sample sources (Table 3), with the mean size of Ghana fish (283 mm FL)

significantly smaller than grey triggerfish from the West Atlantic (Dunnet's T^3 *post hoc*: $P < 0.02$ for both pairwise comparisons). The mean size of West (NC/SC) Independent samples (340 mm FL) was significantly smaller than that of West (SC) Dependent samples (372 mm FL; Dunnet's T^3: $P = 0.016$).

Balistes capriscus size frequency distributions significantly differed for each pair-wise comparison (Table 4; Figure 5). East Atlantic samples had a larger proportion of smaller fish compared to West Dependent samples and West Independent samples. West Dependent *B. capriscus* had a higher proportion of larger fish compared to West Independent samples (Table 4; Figure 5).
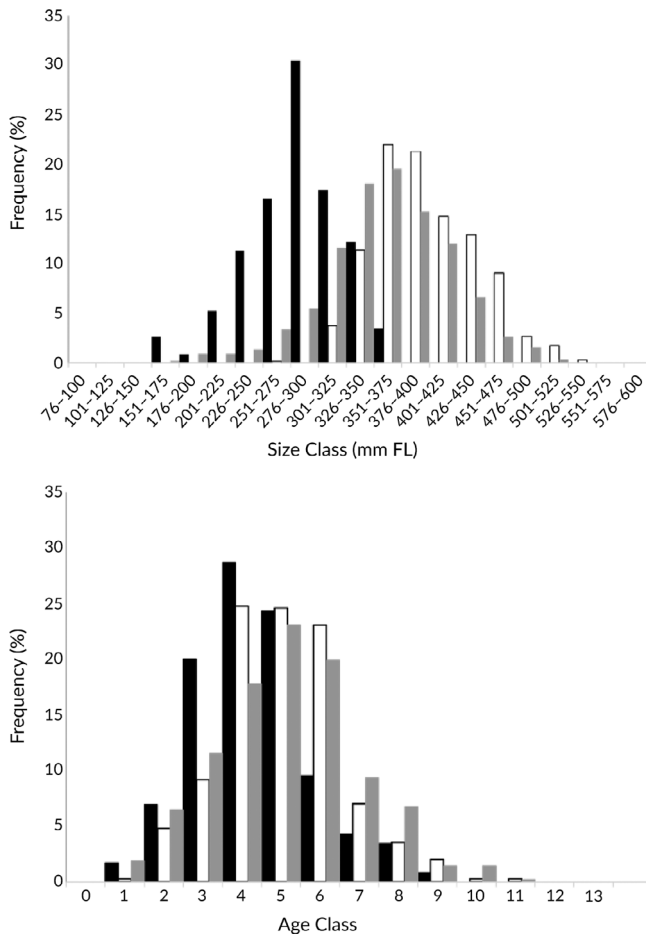
3.2 | Age and growth

Age estimates of *B. capriscus* from East Atlantic samples ranged from 1 to 9 years (mean = 4.3; Table 1; Figure 6). West Atlantic grey triggerfish ranged in age from 1 to 11 years for NC/SC-independent samples (mean = 5.1) and from 1 to 10 years for SC-dependent samples (mean = 4.5; Table 2; Figure 6). Mean age differed among the three sample sources (Table 3), with East Atlantic fish significantly younger than West Independent samples (Dunnet's T^3 *post hoc*: $P < 0.001$), but not significantly different from West Dependent samples (Dunnet's T^3: $P = 0.078$). West Dependent samples were also significantly younger than West Independent samples (Dunnet's T^3: $P < 0.001$). Age frequency distributions differed significantly between East Atlantic and West Independent samples with a higher proportion of West Independent fish in the older age classes (Table 4; Figure 5). Similarly, West Independent fish had a higher proportion of older age classes compared to West Dependent samples (Table 4; Figure 5).

The APE for Ghana samples was 11.3%, for West Dependent samples was 11.4% and for West Independent samples was 12.0%. Sample-source-specific growth curves were fitted, yielding the following von Bertalanffy equations: $L_\infty = 334(1 - e^{-0.47(t + 0.20)})$ for East Atlantic, $L_\infty = 400(1 - e^{-0.63(t + 0.24)})$ for West Dependent, and $L_\infty = 398(1 - e^{-0.41(t + 0.26)})$ for West Independent (Figure 6; Table 5).

3.3 | Comparison between ageing structures

From the West Dependent collections, a total of 240 samples, ranging in size from 231 to 520 mm FL, had age estimates from both spines and otoliths. Age estimates for spines ranged from 1 to 8 years and for otoliths from 3 to 13 (Figure 7). The APE for this sub-set of spines was 11.4% and for the otoliths was 3.0%. An age bias plot indicates that the spine age estimates compared to the otolith age estimates underestimated the ages of *B. capriscus*, starting at age 3 (Figure 8). Structure-specific growth curves were fitted, yielding the following von Bertalanffy equations: $L_\infty = 404(1 - e^{-0.83(t + 0.08)})$ for spines and $L_\infty = 470(1 - e^{-0.31(t + 0.19)})$ for otoliths (Figure 7). The two-factor

FIGURE 5 Size frequency (top) and age frequency (bottom) distributions for *Balistes capriscus* samples examined in the current study from the three sample sources. Size class: ■, East (Ghana); □, West (Dependent); ▨, West (Independent). Age class: ■, East (Ghana); □, West (Dependent); ▨, West (Independent)

TABLE 2 Summary results for grey triggerfish samples collected from East and West Atlantic regions for the current study

	East Atlantic (Ghana)	West Independent (NC/SC)	West Dependent (SC)	West Atlantic (ALL)
Time period	2012–2014	2011–2012	2012–2014	2011–2014
Number of samples	115	416	642	1058
Mean age years ± S.D.; Range	4.3 ± 0.14	5.1 ± 0.09	4.5 ± 0.06	4.8 ± 0.14
	1–9	1–11	1–10	1–11
Mean size L_F mm ± S.D.; range	283 ± 3.7	340 ± 3.1	372 ± 1.8	360 ± 1.7
	166–371	155–518	231–520	157–520

Comparison and source	df	Sum of squares	Mean of squares	F	P
Mean length					
Sample source	2	19.619	9.809	61.9	<0.001
Error	1203	190.452	0.158		
Total	1205	210.071			
Mean age					
Sample source	2	4.431	2.215	14.1	<0.001
Error	1203	189.451	0.157		
Total	1205	193.882			
Spine *vs.* otolith					
Age	3	1.250	0.417	48.9	<0.001
Structure	1	0.552	0.552	64.7	<0.001
Age × structure	3	0.195	0.065	7.6	<0.001
Error		3.233	0.009		
Total		5.102			

TABLE 3 Summary of the three ANOVAs conducted in this study

Note: Mean length was a one-factor ANOVA that tested for significant differences in mean length (mm L_F) among sample sources (East Atlantic, West Independent and West Dependent). Mean age was a one-factor ANOVA that tested for significant differences in mean age among sample sources. Spine *vs.* otoliths was a two-factor ANOVA that tested for significant differences in mean length between ageing structures and among age classes 3–6 (age).

TABLE 4 Pair-wise Kolmogorov–Smirnov test comparison results for size and age frequency distributions between each of the sample sources (East Atlantic, West Independent and West Dependent)

	Size		Age	
	Z	P	Z	P
East *vs.* West Dependent	7.38	<0.001	2.45	0.07
East *vs.* West Independent	4.84	<0.001	2.53	<0.001
Dep *vs.* Ind	3.97	<0.001	3.45	<0.001

ANOVA indicated that mean size varied significantly among the age groups (3–6) and between the structures (Table 3).
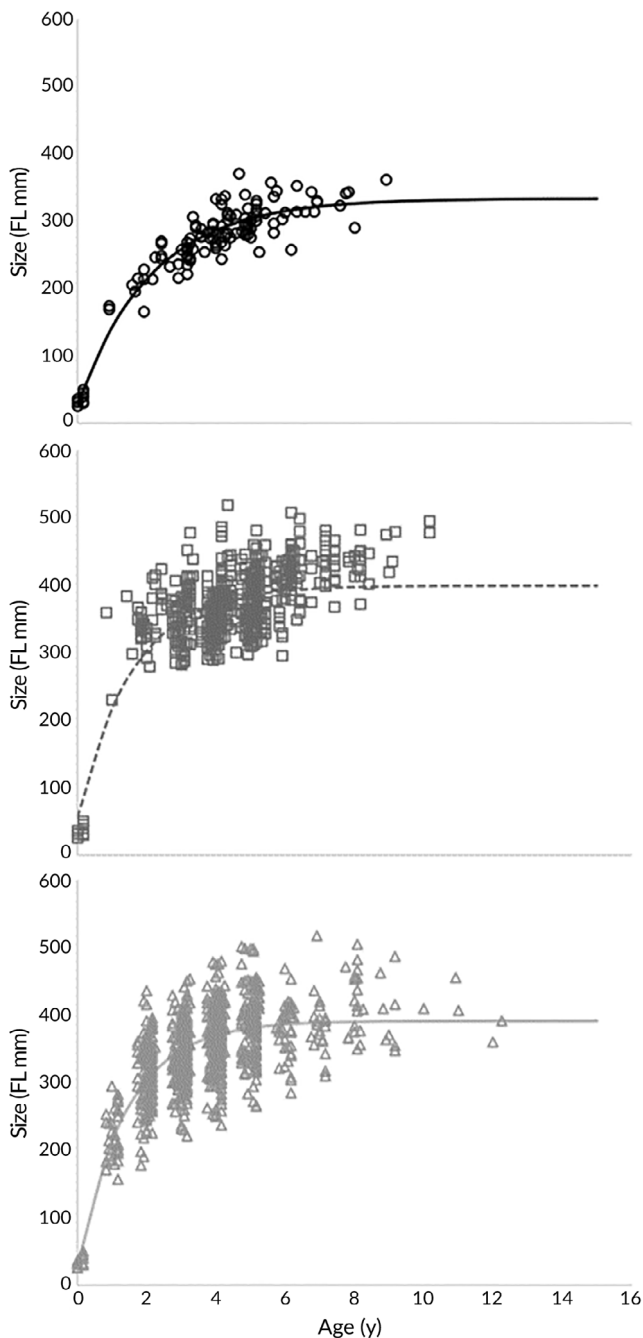
4 | DISCUSSION

This is the first study to directly compare age and growth for a major fisheries species between east and west populations of a transatlantic reef fish. The results obtained from this study provide an updated understanding of growth and age structure of the eastern Atlantic *B. capriscus* population in GOG. The authors also documented that sagittal otoliths can be used to provide age estimates for triggerfish species, and compared to dorsal spines, otoliths as an ageing structure had better between-reader precision.

4.1 | GOG/East Atlantic population

Historically, *B. capriscus* in GOG have been reported in low abundance (Cavérivière *et al.*, 1981). Some researchers have suggested that

throughout the decades of research on GOG *B. capriscus*, the sampled population through time may not fully represent the GOG *B. capriscus* population. Since the 1960s, fish populations in GOG have been monitored mainly *via* bottom and pelagic trawl surveys at depths of 10–300+ m (Koranteng, 2001). Wenner (1971) reported that SEUS benthic trawl surveys of mid-shelf sandy and hard bottom habitats resulted in low catch rates of *B. capriscus* and concluded that trawling was inefficient at collecting benthic reef fish species like *B. capriscus*. Trap and hook-and-line surveys in the same region of the SEUS have consistently caught *B. capriscus* at relatively high abundances (Kelly-Stormer *et al.*, 2017). Therefore, the possibility exists that *B. capriscus* may occur at higher numbers in the GOG region in association with deeper sites, are not efficiently sampled with trawling gear and the few individuals that occur in the 20–60 m depth zone targeted by trawls are using suboptimal habitat, and not representative of the whole population. Nonetheless, in reviewing annual acoustic and trawl survey data for west GOG (Côte d'Ivoire, Ghana, Benin, Togo), the authors noted that *B. capriscus* were only detected at depths of 19–74 m (maximum depth sampled was 300+ m). Of the 1084 *B. capriscus* samples recorded for 1999, 2002, 2005 and 2006, 98% occurred at depths of 60 m or less. Only 19 fish were observed at depths of 65–77 m (Mehl *et al.*, 1999; Mehl *et al.*, 2002; Mehl *et al.*, 2005, 2006). In addition, a portion of the artisanal fishery sector in Ghana uses hook-and-line gear to target reef-associated fishes including species of grouper such as *Epinephelus aeneus* (Geoffroy Saint-Hilaire 1817) and *Epinephelus gigas* (Brünnich, 1768); species of snappers, such as *Lutjanus goreensis* (Valenciennes, 1830) and *Lutjanus fulgens* (Valenciennes, 1830); and species of porgy, such as *Pagellus bellottii* Steindachner, 1882, *Dentex angolensis* Poll & Maul, 1953 and *Dentex congoensis* Poll, 1954, in depths ranging from 10 to 220 m (Aheto *et al.*, 2012; Doyi, 1984; Nunoo *et al.*, 2015). *B. capriscus* are

FIGURE 6 Length-at-ages and von Bertalanffy growth curves for *Balistes capriscus* from the three sample sources in the current study. ——, East (Ghana) Predicted; ○, East (Ghana) Observed; ------, West (SC Dep) Predicted; □, West (SC Dep) Observed; ——, West (FL-NC Ind) Predicted; △, West (FL-NC Ind) Observed
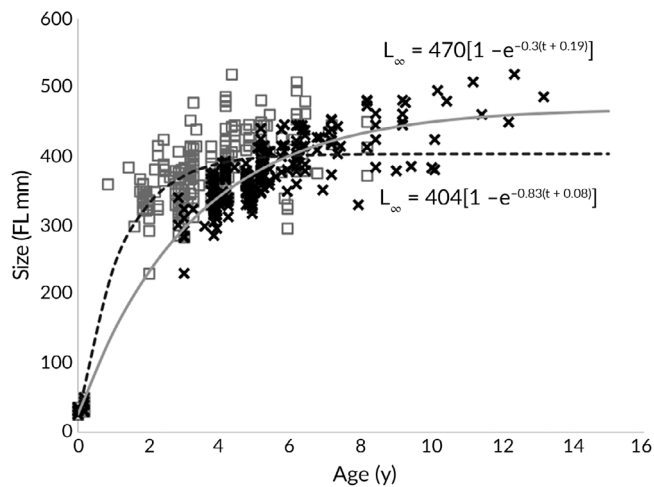
increase overall survival and fecundity by occupying their optimal habitat (Anderson *et al.*, 2013). Many biotic and environmental factors influence the spatial variation in reef fishes' abundance including prey availability (Lee *et al.*, 1991; Verity *et al.*, 1993), recruitment success (Tolimieri, 1995), habitat quality and availability (Sale *et al.*, 1984), temperature (Miller & Richards, 1980; Sedberry & Van Dolah, 1984) and fishing pressure (Koenig *et al.*, 2000; McGovern *et al.*, 1998). During the span of 1963–1992, anomalous spatial and interannual patterns of cooling in coastal waters of GOG were observed and classified into three climatic periods (Koranteng & McGlade, 2001). The first period encompassed the years up to 1972 and was characterized by declining surface and subsurface temperature and low salinity. The second period, from 1972 to 1982, was characterized by colder temperatures, a narrower mixed layer with a shallower than average thermocline, and higher, but less variable salinity. In the third climatic period, post-1982, surface and subsurface water temperatures were high, and salinity was lower and variable (Koranteng & McGlade, 2001). A synchrony occurred in GOG waters with these climatic periods and observed abundance and spatial patterns in the following two fisheries species: round sardine *Sardinella aurita* Valenciennes, 1847, and *B. capriscus*.

Before the early 1970s, the *B. capriscus* population of West African waters in GOG was considered insignificant in number and fish seemed only to occur scattered across the shelf waters as solitary individuals associated with benthic habitats (Caverivière, 1980; Caverivière *et al.*, 1981; Koranteng, 2001). From 1972 to 1978, triggerfish rapidly increased in number, from an estimated biomass of <1 t to a peak of 1,000,000 t. During this period, *B. capriscus* expanded from its solitary benthic existence to also occupying the pelagic zone in massive schools that exhibited migratory behaviour (Caverivière, 1980; Gerlotto, 2017) and became one of the most important species caught in GOG fisheries, particularly in the waters of Côte d'Ivoire, Ghana, Togo and Benin (Caverivière, 1980; Caverivière *et al.*, 1981). *B. capriscus* in GOG did not appear to be limited by habitat-related physical barriers so that when suitable conditions occurred outside its normal benthic habitat, it was able to rapidly increase its zone of distribution into suitable pelagic habitat (Gerlotto, 2017), newly available for triggerfish. The rapid expansion in triggerfish abundance coincided with a decrease in the catch of round sardine, an economically important pelagic commercial species for the region. *S. aurita* landings averaged 25,000 t from 1963 to 1971, peaked at over 72,000 t in 1972 and then crashed and decreased to 1400 t in 1974.
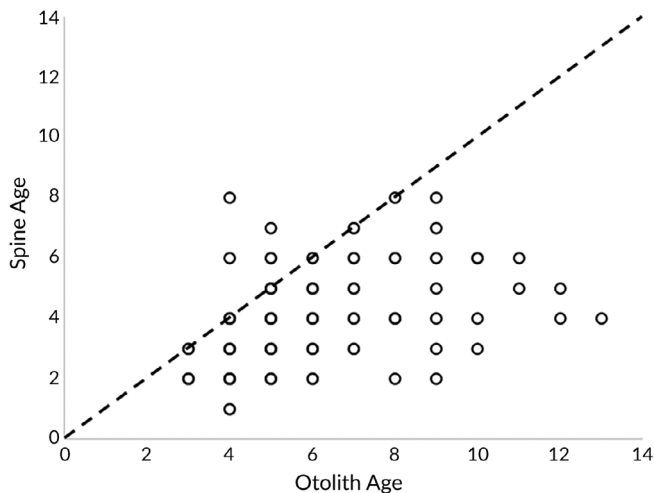
Between 1974 and 1983, during the second climatic period, the sardine fishery was described as "collapsed" (Koranteng & McGlade, 2001; Pezennec, 1994). During this same period, biomass of triggerfish increased rapidly and remained relatively high for several years with an estimated abundance of 314,000–500,000 t, just in the waters of Ghana alone for 1981–1982. Landings for triggerfish in Ghana increased from 2830 t in 1972 to a catch peak of 17,250 t in 1986/1987. Triggerfish biomass decreased rapidly after that peak; landings data analyses indicated that although fishing effort for triggerfish remained unchanged from 1986 to 1991, the triggerfish

rarely caught by Ghanaian artisanal fishers using hook-and-line gear at the hard-bottom sites where these other reef fish species are fished (F Nunoo, unpubl. data). From this information, it appears that *B. capriscus* may not occur at higher abundances in habitats inaccessible to trawling gear.

Shifts in climate impact organisms by changing their environment, and this results in shifts in species distributions and abundances (Hare *et al.*, 2010; Pinsky *et al.*, 2013; Walther *et al.*, 2002). Organisms will

TABLE 5 Summary of age and growth studies on grey triggerfish across the Atlantic Ocean

Study region	Study area and time period	Sample sources (n); age range	L_∞ (mm L_F)	K	t_0	Notes	Study source
Gulf of Guinea	Ghana 2012–2014	FD (115); 1–9	334	0.47	−0.20	Small fish (n = 11) from sargassum included in model as age 0 samples; APE = 11.3	Current study
	Ghana 1980	FI (~50); 1–4	352	0.47	−0.18	No APE reported	Ofori-Danson, 1989
	Cote D'Ivoire, Ghana, Togo, Benin 1999–2004	FI (66); 0–11	391	0.21	−0.29	APE = 8.1	Aggrey-Fynn, 2009
Southeastern Atlantic coast of United States	NC/SC 2011–2012	FI (416); 1–12	398	0.41	−0.26	Small fish (n = 11) from sargassum included in model as age 0 samples; APE = 12.0	Current study
	SC 2012–2014	FD (642); 1–10	400	0.63	−0.24	Small fish (n = 11) from sargassum included in model as age 0 samples; APE = 11.4	Current study
	NC/SC 2011–2014	FI + FD (1058); 1–11	395	0.56	−0.24	Small fish (n = 11) from sargassum included in model as age 0 samples; APE = 12	Current study
	FL-NC 2009–2012	FI (1247); 1–12	382	0.67	0.47		Kelly-Stormer et al., 2017
	FL-NC 1990–2012	FD (6419); 0–15	FE: 457 TO: 436	FE: 0.38 TO: 0.75	FE: −1.58 TO: 0	Adjusted age estimates based on margin; APE ranged from 9 to 12	Burton et al., 2015
Gulf of Mexico of United States	TX-FL 2003–2013	FI + FD (5361); 0–14	484	0.34	−0.06	Included juveniles collected from sargassum; APE = 10.8	Allman et al., 2018
	TX-FL 1996–2000	FI + FD (1625); 0–8	583	0.18	−1.58	Adjusted ages based on margin	Ingram, 2001
	FL 1995–1996	FI + FD (626); 0–14	645	0.15	−1.9		Hood & Johnson, 1997
	FL 1979–1982	FD (2808); 0–13	466	0.38	0.19	Used back-calculated size-at-age	Johnson & Saloman, 1984
Mediterranean Sea	Tunisia 2008–2010	FD (463); 1–5	417	0.24	−0.10	No APE reported	Kacem et al., 2015
Brazil	São Paulo 1984–1985	FD (1503); 1–5	510	0.27	−0.12	Concluded two increments form per year based on margin increment analysis; used back-calculated size-at-age; no APE reported	Bernardes, 2002

FIGURE 7 Comparison of the length-at-age and von Bertalanffy growth curves for the same set of samples based on age estimates from the first dorsal spine *vs.* the sagittal otolith. □, Spine Observed; ×, Otolith Observed; -----, Spine Predicted; ——, Otolith Predicted

FIGURE 8 Age bias plot comparing the age estimates from the sagittal otolith and dorsal spine of individual fish samples. The dashed line represents exact agreement of structures for age estimates

landings decreased to <1 t by 1990 and the catch remains around that level today. In the third climatic period, *S. aurita* entered a "prosperous" phase in which landings increased to a peak of 154,000 t by 1992 (Koranteng & McGlade, 2001, Pezennec, 1994).
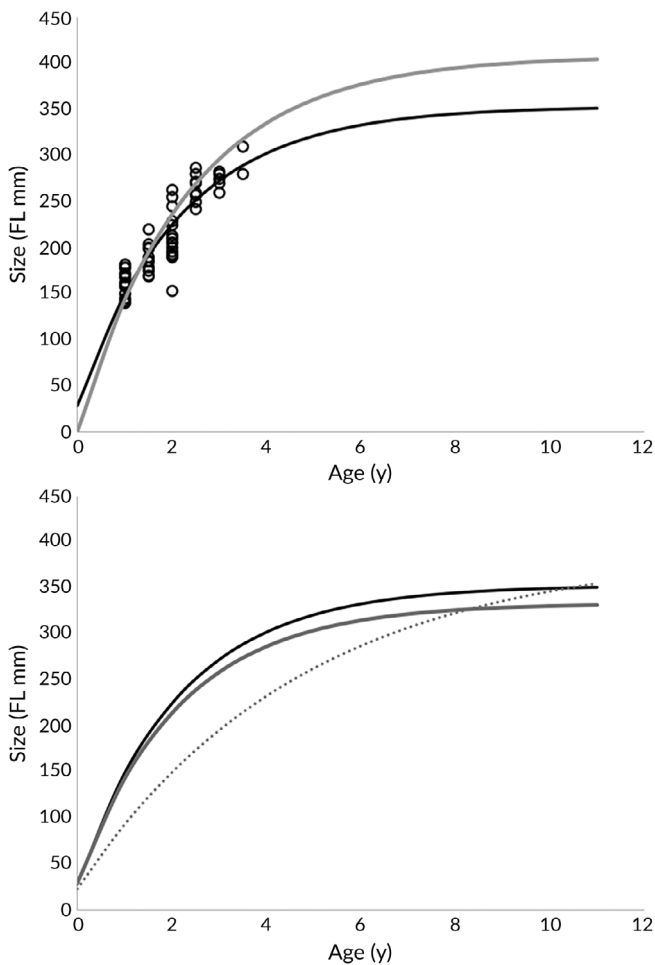
Water temperature seems to be an important factor in the distribution of *B. capriscus* (Muhling *et al.*, 2014). The second climatic period consisted of cooler and more stable waters, which may have enhanced some aspects of the environment for *B. capriscus* (Koranteng & McGlade, 2001). Scientists noted that in addition to increasing in abundance within its benthic habitat, *B. capriscus* expanded into pelagic habitat (Koranteng, 1998). To achieve this population explosion, *B. capriscus* prey availability would also have increased, either in the benthic zone, pelagic zone or both. *B. capriscus* has a broad diet and is considered an opportunistic carnivore (Aggrey-

Fynn, 2007; Blitch, 2000; Dance *et al.*, 2018; Goldman *et al.*, 2016). Although most triggerfish diet studies emphasize the benthic prey items found in their stomachs, many studies have noted that pelagic gastropods (pteropods) appear to be an important food resource for this species (Dance *et al.*, 2018, Goldman *et al.*, 2016). A 2005 diet study from GOG reported that *B. capriscus* across a range of sizes (117–449 mm FL) fed on a variety of pelagic prey items such as copepods, euphausids, mysids, anthomedusa, jellyfish and fish larvae (Aggrey-Fynn, 2007).

The fishing methods used to obtain market fish in GOG waters have remained relatively unchanged over the past 40 years (Koranteng, 2001; Nunoo *et al.*, 2014). Triggerfish are mainly caught using a combination of trawls and purse seines (Aggrey-Fynn, 2013; Cavervière *et al.*, 1981; Koranteng, 2001). During the climatic period in which increased *B. capriscus* abundance occurred (1972–1983), Ofori-Danson (1989) investigated age and growth of fish obtained in 1980 with bottom trawls from the waters of Ghana at depths of 15–50 m. A total of 55 samples (out of 658 total) were aged and used to estimate von Bertalanffy growth parameters using an "eye-fitted" curve (Table 1; Figure 9). The maximum size of *B. capriscus* in that study was 338 mm FL and maximum estimated age was 4 years (Ofori-Danson, 1989). To compare the growth parameters from the 1980 samples with the current study, the authors reconstructed the size at age data using the figure provided in Ofori-Danson (1989), then recalculated the von Bertalanffy growth function using the same least squares method described in the methods of this study. The asymptotic mean size decreased from the "eye-fit" value of 408 to 352 mm FL, K increased slightly from 0.43 to 0.47 and t_0 shifted from a fixed value of 0 to a freely calculated value of −0.18 (Table 1; Figure 9).

A second growth study of GOG triggerfish occurred in 2005, 19 years after the population abundance peaked in 1986, and then crashed (Aggrey-Fynn, 2009). That study used mainly bottom trawl sampling, but did include a few pelagic trawl collections to obtain a total of 84 triggerfish ranging in size from 123 to 449 mm FL from depths of 23–60 m. Age estimates were reported for 66 of the samples and ranged from 1 to 11 years (Table 1). von Bertalanffy growth parameters were also estimated for the 2005 samples; L_∞ increased to 392 mm FL and maximum size increased to a new record of 449 mm FL (Table 1; Figure 9).

The current study also focused on *B. capriscus* samples caught with bottom trawls at depths of 20–55 m, similar to the 1980 samples (Ofori-Danson, 1989). The sample size of this study was larger (n = 115) than the previous studies, but size range of samples overlapped (166–371 mm FL) and the estimated ages (1–9) of this study were similar in range to those from the 2005 population (Aggrey-Fynn, 2009). Direct comparisons of von Bertalanffy growth parameters among studies can be difficult because of differences in the methods used to apply the growth function and differences in study design/sample collection. Directly comparing von Bertalanffy parameters among populations may be inappropriate (Zivkov *et al.*, 1999). Zivkov *et al.* (1999) recommended the simple, more biologically relevant approach of comparing mean lengths of fish at the same age up to the maximum age of the youngest population. The authors of this

FIGURE 9 von Bertalanffy growth curves for *Balistes capriscus* from eastern Atlantic waters. Length-at-age data from 1980 (top graph) reported by Ofori-Danson (1989) was originally used to calculate a growth curve using a mean eye-fitted method; the observed data are also plotted here using the same methods applied to data for the current study. Von Bertalanffy growth curves (bottom graph) from each of the three sampling periods in East Atlantic waters are illustrated here for comparison. ○, 1980 Observed; ——, 1980 Predicted; ——, 1980 Mean Eye-Fitted; ——, 1980 Predicted; ·······, 2005 Predicted; ——, 2012–2014 Predicted

TABLE 6 Mean length (mm L_F) of samples in each age class

Age	Ghana 1980[a]	Ghana 2012–2014[b]
0	—	—
1	176	172
2	229	211
3	280	252
4	310	288
5	—	300
6	—	316
7	—	326
8	—	325
9	—	362

[a]Ofori-Danson (1989).
[b]Current study.

Atlantic Ocean. Such a comparison is complicated within the context of this study due to at least two factors: the difficulty in estimating ages for this species and the differences in fish sampling methods used between the two regions. The observed differences in age and growth between the populations in this study cannot be easily attributed to differences in how dorsal spines were interpreted. Because of the well-reported difficulties in using the dorsal spine to age triggerfish, Burton *et al.* (2015) noted that a robust set of criteria for interpreting spine increments was established at a SEUS regional workshop. Readers of the triggerfish spines in the current study participated in that workshop, aided in establishing the criteria and used those criteria for the current study. Nonetheless, the APE for *B. capriscus* spines across studies using the criteria are still relatively high, ranging from 9 to 12% (Table 5; Burton *et al.*, 2015, Kelly-Stormer *et al.*, 2017).

The second factor that makes comparisons between the populations difficult is that samples were obtained using different gears; fish from the west were collected with a combination of traps and hook-and-line and fish from the east were collected with trawls. Several studies have noted the impacts of gear selectivity on estimates related to size, age and growth in triggerfishes (Allman *et al.*, 2018; Rivera Hernández *et al.*, 2019; Thomas, 2018). One way to reduce gear-related biases of population estimates is to combine samples caught by multiple gears (Allman *et al.*, 2018; Wilson *et al.*, 2015). In the current study, the authors purposefully included triggerfish samples in the west from both fisheries-independent and -dependent collections, so that they could reduce impacts of gear selectivity because West Dependent samples were caught *via* hook-and-line and West Independent samples were caught with traps. When examining the differences between the West Dependent and West Independent samples in this study, the authors did document typical gear-related biases; mainly West Dependent *B. capriscus* samples were significantly larger and younger compared to West Independent samples. A study on age and growth of *B. capriscus* from GOM documented similar differences between fisheries-dependent and -independent samples (Allman *et al.*, 2018). As stated earlier, East

study were able to obtain mean length data for ages 1–4 from the 1980 samples to compare with 2012–2014 mean lengths (Table 6). During the 1973–1987 period of rapid increase in *B. capriscus* abundance, when fish expanded into new habitat and were fished heavily, mean sizes at ages 1–4 were larger than East Atlantic fish from the current study, indicating that fish grew faster, attaining a larger size at age compared to fish examined in the current study.

4.2 | Comparison between East and West Atlantic populations

The current study includes comparing demographic and life-history attributes of *B. capriscus* between populations from the East and West

Atlantic triggerfish samples were caught *via* trawls, yet another sampling gear. Nonetheless, as explained in the previous section, trawling in that region seems to obtain a representative sample of the overall *B. capriscus* population in the GOG. Ultimately, the authors cannot fully ensure that differences in gears used to obtain fish samples between the east and west populations had no impact on differences documented between the populations. Therefore, they have limited their comparisons to a few general trends.

The comparison between GOG and SEUS *B. capriscus* populations resulted in two notable major differences. Maximum size and age of GOG *B. capriscus* have consistently been lower when compared to the SEUS population. Sampling efforts of GOG triggerfish collected in the 1970s and 1980s reported a maximum size of 340 mm FL and maximum estimated age of 4 years (Tables 1 and 5; Ofori-Danson, 1989). Around that same time period of collection, the maximum size and age reported for SEUS *B. capriscus* were 585 mm FL and 13 years, respectively (Escorriola, 1991). In the 1990s and early 2000s, maximum size and age for GOG increased to 446 mm FL and 11 years (Table 1; Aggrey-Fynn, 2009), which was still smaller and younger than the maximum size (578 mm FL) and age (13 years) reported for SEUS over the same period of collection (Kelly-Stormer *et al*., 2017). Similarly, when comparing the maximum size and age from the current study, GOG fish continued to maintain a smaller maximum size and age compared to SEUS (Table 2). Several mechanisms may contribute, in part and in combination, to the observed differences between east and west *B. capriscus* population attributes. The authors of this study have selected two of those to discuss further: (a) genetic divergence of populations and (b) latitudinal environmental gradients.

The GOG *B. capriscus* population appears to be genetically distinct from other Atlantic populations with evidence of minimal connectivity to West Atlantic SEUS fish or northeastern Atlantic fish (Saillant & Antoni, 2014). The GOG population is characterized by significantly lower haplotype diversity, lower nucleotide diversity and a smaller effective population size compared to fish from SEUS and the Mediterranean Sea (Saillant & Antoni, 2014). Fish samples analysed from GOG contained distinct and derived mtDNA haplotypes which may suggest an ancient founder event (Saillant & Antoni, 2014). Biological traits of a species, including maximum size and age, may diverge within isolated populations exposed to differing selective pressures (Feder *et al*., 2012; Gaither *et al*., 2015; Pelc *et al*., 2009). A more extensive examination of genetic differences among the populations of *B. capriscus* occurring throughout the eastern and western Atlantic is needed to fully evaluate the role of genetics in determining population attributes.

Balistes capriscus occur in abundance across a wide range of latitudes in the eastern and western Atlantic (Figure 1). In the east, it contributes to fishery landings as far as 43° N in the Adriatic Sea off the coast of Croatia (Dulcic & Soldo, 2005), at 37–38° N off the coast of Portugal (Simoes *et al*., 2013; Veiga *et al*., 2010) and in waters of the Azorean archipelago (Diogo & Pereira, 2014), around 36° N in Iskenderun Bay (İşmen *et al*., 2004), and at 34° N in the Gulf of Gabès, off the coast of Tunisia (Kacem *et al*., 2015; Kacem & Neifar, 2014). *B. capriscus* is found in the tropical latitudes in the east from 15° N off

the coast of Senegal down to 15° S in waters of Angola (Fischer *et al*., 1981). In the western Atlantic, *B. capriscus* is common from 37° N off the coast of Virginia, U.S.A., down to around 27° N off eastern Florida, throughout GOM and the Caribbean Sea from around 30° N in the northern GOM to 18° N in waters of the Chinchorro Bank Biosphere Reserve of the Yucatan (Castro-Pérez *et al*., 2018). *B. capriscus* also occurs in the western Atlantic down to 25° S off southern Brazil (Bernardes, 2002; Bernardes & Dias, 2000). Several studies have documented a latitudinal gradient relating to size and longevity in ectotherms (Atkinson, 1994; Atkinson & Sibly, 1997). Maximum size and age in many fish taxa increase with increasing latitude and decreasing temperature (Choat *et al*., 2003; Lek *et al*., 2012; Meekan *et al*., 2001; Pauly, 1978). *B. capriscus* populations may conform to this general trend. The East Atlantic population examined in this study occurred at a latitude of 4° N and exhibited maximum size and age of 446 mm FL and 11 years, respectively. *B. capriscus* populations from higher latitudes had larger maximum sizes: a maximum size of 610 mm FL was reported from 18° N in waters of the Chinchorro Bank Biosphere Reserve of the Yucatan (Castro-Pérez *et al*., 2018); in GOM and SEUS from around 27 to 35° N, maximum reported sizes range from 578 to 670 mm FL (Allman *et al*., 2018; Kelly-Stormer *et al*., 2017). Maximum reported ages of 14–15 years for GOM and SEUS (Allman *et al*., 2018; Burton *et al*., 2015) are also higher than the maximum age of 11 years for GOG (Aggrey-Fynn, 2009). Further research is needed to identify potential underlying environmental drivers between the East and West Atlantic regions that may influence differences in the population demographics of *B. capriscus*.

4.3 | Sagittal otoliths as an alternative to spines for triggerfish species

Two main areas of evaluation contribute to the overall error in estimating age and growth of fish populations: accuracy and precision of the age estimates obtained from ageing structures/methods (Beamish & Fournier, 1981; Campana, 2001). Accuracy is assessed through validation or verification. Age validation in fish species populations directly evaluates the number of growth zones present in an ageing structure compared to the known age of that fish. Verification indirectly assesses age accuracy through evaluating the periodicity trends of a sampled population by examining the monthly proportion of individuals that have the slower growing zone contained within the last increment formed on the edge of the ageing structure (Campana, 2001).

Several studies used marginal increment analysis to indirectly verify that one increment forms per year in the dorsal spine of *B. capriscus* (Burton *et al*., 2015; Kelly-Stormer *et al*., 2017). Nonetheless, studies on other species that used known-age fish showed that external bony structures do not continue to accumulate increments regularly each year throughout the life of a fish (Buckmeier *et al*., 2002; Buckmeier *et al*., 2012; Gu *et al*., 2013). In addition, a study on *B. capriscus* used oxytetracycline to chemically mark 12 fish and then held them in tanks for 1 year before processing them for age

determination (Hood & Johnson, 1997). Although all 12 fish increased in size after 1 year, no growth occurred in the dorsal spine past the chemical mark which was still on the edge of all 12 spines. The fish used in that study were all relatively large adults (Hood & Johnson, 1997). This may indicate that triggerfish dorsal spines do not always reflect the true age of a fish. Studies on three species of gar (Lepisosteidae) and a species of catfish (Ictaluridae) showed a similar occurrence when comparing otoliths *vs.* external structures of chemically marked fish of known ages. The spines and fin rays in catfish and gars did not consistently continue to accrue annual increments, whereas the otoliths of the same samples did (Buckmeier *et al.*, 2002; Buckmeier *et al.*, 2012; Buckmeier *et al.*, 2018).

Precision is a measure of repeatability and can be examined *via* the index of APE that measures the agreement of age estimates between readers (Beamish & Fournier, 1981). A low APE means that readers independently obtained similar counts of the growth zones, and this signifies higher precision. In most fish species, an acceptable APE is <5% (Campana, 2001). Nonetheless, APE reported for triggerfish studies ranges from 9 to 12% (Allman *et al.*, 2018; Burton *et al.*, 2015; Kelly-Stormer *et al.*, 2017). In this study, the authors also had APE for spines ranging from 11 to 12%, but the APE for otoliths was 3%. A triggerfish dorsal spine is an external bony structure used in defence and often will contort, twist and even break during a fish's lifetime, rendering many spines to have unclear increments that may contribute to the higher between-reader APE (lower precision overall) for triggerfish species (Kelly-Stormer *et al.*, 2017). Otoliths are internal ossified structures and not impacted by the external physical forces acting on the outside of a fish (Campana, 1999).

Balistes capriscus samples have been aged using the first dorsal spine for over 30 years. The main reason for this is because it is an easy structure to obtain relative to triggerfish otoliths, which are small, fragile and comparatively more difficult to extract. Research comparing precision and accuracy of external ageing structures in fishes to otolith-based age estimates shows that those structures (spines, fin rays and scales) can significantly underestimate the true age of a fish (Buckmeier *et al.*, 2002, Buckmeier *et al.*, 2012, Gu *et al.*, 2013). The comparison between spines and otoliths in this study is preliminary, with a sample size of only 240 fish, and further evaluation is necessary. Nonetheless, the results of this study showed that otoliths can be effectively extracted, and that the sagittal otoliths do contain increments. The APE for otoliths from this study was lower than spines, indicating that using otoliths for this species may improve precision. The authors also found that dorsal spine increment counts may underestimate the true age in this species compared to otoliths. The results of this study, combined with preliminary bomb radiocarbon age validation results of otolith-based age estimates for GOM *B. capriscus* (Patterson *et al.*, 2019), provide further evidence that external bony structures may underestimate age in fish population growth studies. A large study on ageing error is currently underway in GOM *B. capriscus* comparing otolith and spine age estimates (W. Patterson, Univ. of FL, pers. comm.), and results from that work should further elucidate the accuracy and precision of ageing structures for triggerfish species.

AUTHOR CONTRIBUTIONS

V.R.S. initiated the concepts for this paper, collected the FD triggerfish samples, conducted the data analyses and composed the initial draft. J.M.R.H. assisted in obtaining age estimates from spines and otoliths of triggerfish samples and provided feedback on paper organization and essential editorial comments on the final draft. F.K.E.N. co-conceived this work, provided samples from GOG, assisted in the initial writing of the paper and edited the final draft.

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