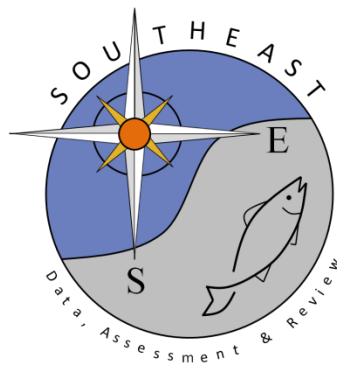


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Factors affecting estimates of size at age and growth in grey triggerfish *Balistes capriscus* from the northern Gulf of Mexico

R. J. ALLMAN*†, W. F. PATTERSON III‡, C. L. FIORAMONTI§ AND
A. E. PACICCO||

*National Marine Fisheries Service, Southeast Fisheries Science Center, Panama City Laboratory, 3500 Delwood Beach Road, Panama City, FL 32408, U.S.A. , ‡Department of Fisheries and Aquatic Sciences, University of Florida, 7922 NW 71st Street, Gainesville, FL 32653, U.S.A., §Natural Science Division, Gulf Coast State College, 5230 West Highway 98, Panama City, FL 32401, U.S.A. and ||Riverside Technologies Inc., National Marine Fisheries Service, Panama City Laboratory, 3500 Delwood Beach Road, Panama City, FL 32408, U.S.A.

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Growth zones in dorsal spines of grey triggerfish *Balistes capriscus* from the northern Gulf of Mexico were utilized to estimate growth and examine factors that may affect estimates of size at age. Age was estimated from dorsal-spine sections of 4687 individuals sampled from U.S. waters during 2003–2013, including both fishery-independent ($n = 1312$) and fishery-dependent ($n = 3375$) samples. Ninety-six per cent ($n = 4498$) of these sections were deemed suitable for ageing; average per cent error between two independent readers was 10.8%. Fork length (L_F) ranged from 65 to 697 mm and age estimates from 0 to 14 years. Both sex and sample source (fishery-independent v. recreational) significantly affected estimated size at age for 2–6 year-old fish. Data were pooled between sources to fit sex-specific von Bertalanffy growth functions. Results for the female model were $L_\infty = 387$ mm L_F , $k = 0.52$ year⁻¹ and $t_0 = 0.01$ year, while for males $L_\infty = 405$ mm L_F , $k = 0.55$ year⁻¹ and $t_0 = 0.02$ year. These results were significantly different between sexes and indicate clear sexual dimorphism. Thus, growth should be modelled separately by sex when examining population parameters or conducting stock assessment modelling. The positive bias in estimates of size at age computed for recreational v. fishery-independent samples also has clear implications for stock assessment as growth functions computed with fishery-dependent samples would tend to overestimate stock productivity.

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Key words: dorsal spines; gear selectivity; sexually dimorphic growth; von Bertalanffy growth function.

INTRODUCTION

Globally, reef-fish populations are affected by myriad anthropogenic stressors, such as habitat destruction (Coker *et al.*, 2014; Holbrook *et al.*, 2015), invasive species (Green *et al.*, 2012; Johnston & Purkis, 2016) and overfishing (Hughes, 1994; Friedlander & De Martini, 2002). With respect to overfishing, quantitative estimates of stock

†Author to whom correspondence should be addressed. Tel.: +1 850 234 6541; email: robert.allman@noaa.gov

productivity, spawning biomass or potential yield are often elusive for many reef-fish fisheries. The lack of data on biological characteristics, landings or other data inputs necessary for quantitative stock assessments is problematic given the requirement of the Magnuson–Stevens Conservation and Management Act (U.S.D.C., 2007) to establish annual catch limits (ACL) for all stocks listed in U.S. fishery management plans (FMP).

Gulf of Mexico (GOM) grey triggerfish *Balistes capriscus* Gmelin 1789, is an example of a previously data-moderate stock for which extensive research effort has been expended to estimate biological parameters to facilitate stock assessment. This species inhabits tropical and temperate waters from Norway to the north-western coast of Africa in the eastern Atlantic Ocean (Ofori-Danson, 1989) and from Nova Scotia to Argentina in the western Atlantic Ocean, including waters of the GOM and off Bermuda (Briggs, 1958). In the GOM, *B. capriscus* support important commercial and recreational fisheries, with landings increasing in the 1980s and 1990s, in part due to increased regulations on other reef fishes, such as snappers and groupers (Valle *et al.*, 2001; Bernardes, 2002). Declining landings thereafter were, however, cause for concern given continued high recreational and commercial effort targeting northern GOM reef fishes (SEDAR, 2006). The most recent stock assessment determined that *B. capriscus* were overfished and in 2013 commercial and recreational catch limits were reduced and a fixed closed season was established (SEDAR, 2015).

Balistes capriscus are managed as a single stock in the U.S. GOM by the Gulf of Mexico Fishery Management Council (GMFMC; <https://www.federalregister.gov/documents/2017/09/15/2017-19644/gulf-of-mexico-fishery-management-council-public-meeting>), with early stock assessments employing surplus production modelling (Goodyear & Thompson, 1993; Valle *et al.*, 2001). The lack of age data, which precluded age-based assessments, was because *B. capriscus* have small and difficult to extract otoliths. As an alternative ageing structure, validation of annual growth zone formation in *B. capriscus* dorsal spines (Allman *et al.*, 2016) has enabled those structures to be utilized to compute growth functions and age–length keys required for age-structure assessment models (SEDAR, 2006, 2015). One caveat to this is the microstructure of *B. capriscus* spine sections can be more difficult to interpret as compared with typical bony fish otoliths, thus there is potential for disagreement in age estimates between readers.

The objective of the current study was to test factors, including between-reader precision, that potentially could affect estimates of size at age, hence growth, in *B. capriscus*. Differences in estimated size at age were examined between fishery-independent samples and those from fishery landings to examine if fishery selectivity could potentially affect growth estimates. Also, data were tested for sexually dimorphic growth in *B. capriscus* given evidence that males grow faster than females in the South Atlantic Ocean (Kelly-Stormer *et al.*, 2017) and GOM (Ingram, 2001; Simmons & Szedlmayer, 2012). Results of these analyses are discussed in the context of examining *B. capriscus* population ecology and potential biases in stock assessments.

MATERIALS AND METHODS

Balistes capriscus were sampled each month from January 2003 to December 2013 from recreational, commercial and fishery-independent landings. In total, 4687 grey triggerfish were sampled from fishery-independent surveys (28%) and recreational (38%) and commercial (34%)

TABLE I. Number of *Balistes capriscus* collected from the Gulf of Mexico by year, fishing mode and gear type

Year	Commercial			Recreational		Fishery-independent				Total
	HL	LL	SP	HL	SP	HL	TP	TWL	SP	
2003	43	43		52	2	3	10			153
2004	24	16		108		10	8		10	176
2005	82	55		65		14	74			290
2006	22	52		83			119			276
2007	18	49		62		34	61			224
2008	9	67		217	15	13	90	43	1	455
2009	30	21		260	10	26	209	96		652
2010	17	16		162	3	26	51	73		348
2011	142	53		104	4	28	61	22		414
2012	291	18		180	1	122	40	42		694
2013	460	35	14	465		4	24	3		1005
Total	1138	425	14	1758	35	280	747	279	11	4687

HL, hook and line; LL, bottom longline; SP, spear; TP, chevron trap; TWL, benthic trawl.

TABLE II. Number of *Balistes capriscus* collected from the Gulf of Mexico by fishing mode, gear type and state landed

Source	Alabama	Florida	Mississippi	Louisiana	Texas	Total
Commercial hook and line		532		605	1	1138
Commercial longline		425				425
Commercial spear		14				14
Recreational hook and line	186	1549		5	18	1758
Recreational spear	1	26		1		28
Fishery-independent hook and line	4	271		2	3	280
Fishery-independent trap		744			3	747
Fishery-independent trawl	2	172		30	75	279
Fishery-independent spear		11	7			18
Total	193	3744	7	643	100	4687

landings (Table I). Fish were collected with hook and line (fishery independent, size 1/0 hooks), bottom longline (generally size 12/0–15/0 hook), spear, chevron trap and benthic-trawl gear. *Balistes capriscus* were collected throughout the U.S. GOM, but most (80%) were sampled from the west Florida Shelf (Table II). Recorded capture depths ranged from 6 to >100 m. Fish were measured to the nearest mm fork length (L_F) and weighed (M) to the nearest 0.01 kg and their sex determined macroscopically when they were landed whole. Capture depth was recorded from most fishery-independent landings and from a small number of fishery-dependent landings. The first dorsal spine was extracted for age determination by inserting a knife just posterior to the spine and cutting medially *c.* 2.5 cm into the fish. Another identical cut anterior to the spine effectively cut out a notch of flesh that included the entire condyle of the spine. Dorsal spines were prepared for sectioning by boiling in water for 1 min to remove soft tissue and scraping the posterior groove free of tissue. Each spine was glued to cardstock and three transverse sections (0.5–0.7 mm thickness) were cut simultaneously with four 10 cm diamond coated blades on an Isomet low-speed saw (www.buehler.co.uk). Prepared sections were fixed to microscope slides with mounting medium.

Spine sections were viewed with a dissecting microscope under 10–40× magnification with transmitted light and the number of translucent zones present were counted without knowledge of when the fish was sampled or L_F . Opaque zones representing faster growth are relatively wide and zones corresponding to slow growth periods are narrow and appear translucent under transmitted light (Lessa & Duarte-Neto, 2004; Allman *et al.*, 2016). Counts of translucent zones in *B. caprisicus* spine sections represented integer ages in years, given recent annual formation verification and validation reported by Allman *et al.* (2016). A sub-set of spine sections ($n = 2348$) was read independently by a second reader and average per cent error (APE) in translucent zone counts between readers was computed with the method of Beamish & Fournier (1981): $N^{-1} \sum_{j=1}^N \left[R^{-1} \sum_{i=1}^R (X_{ij} - X_j) X_j^{-1} \right]$, where N is the number of sample ages, R is the number of times fish was aged, X_{ij} is the i th age determination of the j th fish and X_j is the average age calculated for the j th fish. Average per cent error also was computed between readers for a reference collection of *B. caprisicus* spine sections ($n = 115$) prepared to assess reader agreement and ageing accuracy.

The margin of each spine section was recorded as translucent or opaque by the primary reader and a readability code of good, fair, difficult, poor processing or unreadable was assigned. The number of opaque zones visible including any partial opaque zone on the margin was used to assign a calendar age. Fractional age was determined by calculating fractional year using the equation: absolute value [(capture date – spawning date)365⁻¹]. The peak spawning date was set at July 1, based on *B. caprisicus* spawning indicators (Ingram, 2001; Kelly-Stormer *et al.*, 2017). Fractional year was added to calendar age if capture date was after July 1 or subtracted if capture date was before.

A three-factor fully-crossed analysis of variance (ANOVA) model was computed to test the effects of sex and sample source (recreational *v.* fishery-independent) on estimated size at age for ages 2–6 years, the most prevalent age classes present in the data. Recreational samples were chosen for comparison to fishery-independent samples since size distributions were similar between these sources and sex was recorded for these observations. The dependent variable in the model, L_F , was ln-transformed to meet parametric assumptions. The three-way interaction term (age × sex × source) was sliced by source to test for sex-specific differences in size at age by sample source and was sliced by sex to test for differences between fishery-independent *v.* recreational estimates of size at age by sex. A χ^2 goodness-of-fit test was used to determine if sex ratios were significantly different from 1:1.

von Bertalanffy growth functions (VBGF) were fitted to L_F at fractional age data with the method of least squares using the solver function in Microsoft Excel 2010 (Haddon, 2001): $L_t = L_\infty [1 - e^{k(t-t_0)}]$, where L_t is the L_F at time of capture, L_∞ is asymptotic L_F , k Brody's growth coefficient and t_0 is the hypothetical age at which $L_F = 0$. Models were fit for the full data set and for males and females separately. Data from 863 age 0 *B. caprisicus* captured in neuston nets during 2000–2004 were included in a model that contained both sexes to test whether their inclusion significantly affected VBGF fit, which was tested with a likelihood ratio test (Cerrato, 1990). Fractional age for these juveniles was calculated as described above. Sex-specific VBGF models were computed, with both models incorporating the age 0 samples and then a likelihood ratio test was computed to test whether VBGFs were significantly different between sexes.

RESULTS

Fork length ranged from 65 to 697 mm. Commercial longline samples had the greatest mean L_F (488 mm L_F), followed by commercial hook and line (404 mm L_F) and recreational hook and line (365 mm L_F) [Fig. 1(a)]. Fishery-independent gears collected the smallest individuals [mean L_F : hook and line 321 mm L_F ; chevron trap 297 mm L_F ; benthic trawl 195 mm L_F ; Fig. 1(b)]. Sex was recorded from 53% of individuals, nearly all of which were recreational and fishery-independent samples, since commercial landings are typically eviscerated at sea. Females outnumbered males by

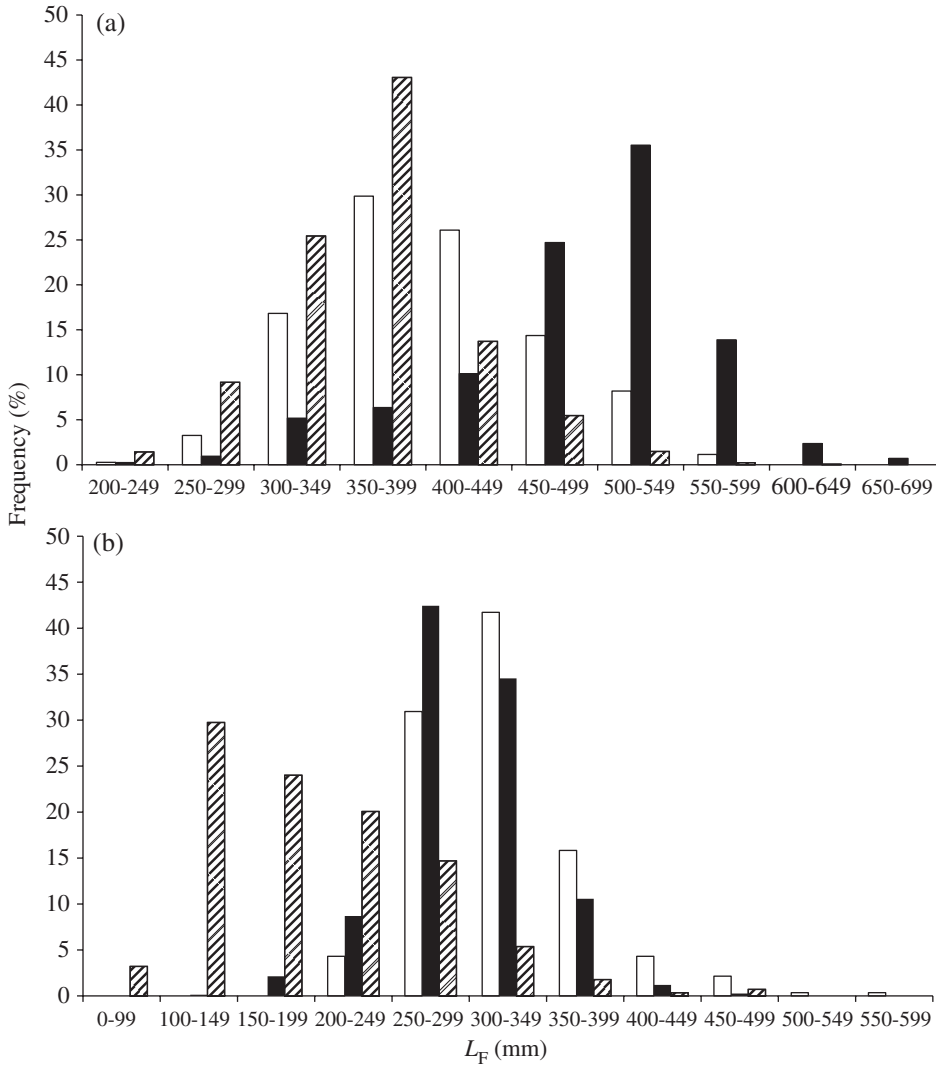


FIG. 1. (a) Fishery-dependent (\square , commercial hook and line, $n = 1135$; \blacksquare , commercial longline, $n = 425$; \boxtimes , recreational, $n = 1758$) and (b) fishery-independent (\square , hook and line, $n = 278$; \blacksquare , trap, $n = 747$; \boxtimes , trawl, $n = 279$) fork length (L_F)-frequency distribution for *Balistes capriscus* from the Gulf of Mexico 2003 to 2013.

a ratio of 1.6:1 for all gear types combined and a χ^2 goodness-of-fit test indicate that this ratio was significantly different from a 1:1 ratio ($\chi^2 = 70.4$, $P < 0.001$).

AGE

It was possible to estimate age for 4498 (96%) of the 4687 dorsal spine sections examined. The APE between primary and secondary readers was 10.8%, while APE was 9.1% between both readers and accepted ages for the *B. capriscus* spine section reference set. Among study samples, estimated age ranged from 0 to 14 years. Differences

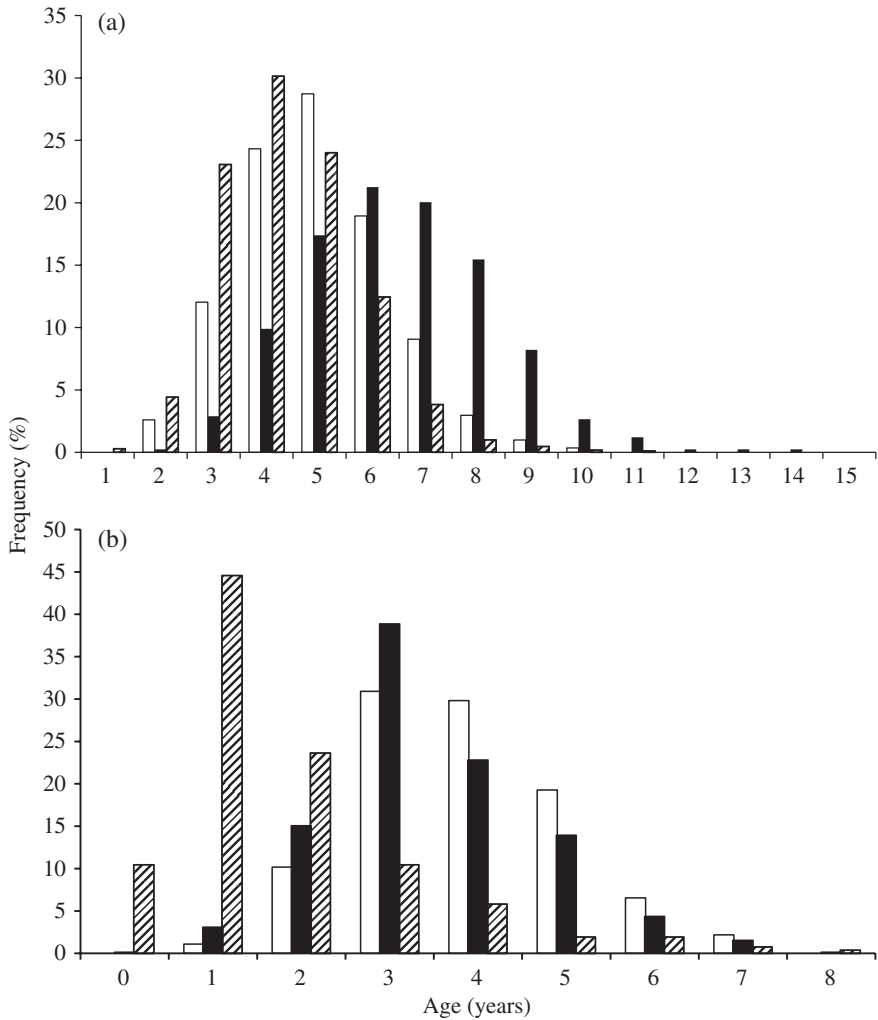


FIG. 2. (a) Fishery-dependent (\square , commercial hook and line, $n = 1114$; \blacksquare , commercial longline, $n = 414$; \square , recreational, $n = 1695$) and (b) fishery-independent (\square , hook and line, $n = 275$; \blacksquare , trap, $n = 710$; \square , trawl, $n = 258$) age frequency distribution for *Balistes capriscus* from the Gulf of Mexico 2003 to 2013.

were noted between fishing modes and gear types with the commercial longline samples having the highest mean age followed by the commercial hook-and-line fishery and recreational fishery [6.5, 5.0 and 4.4 years, respectively; Fig. 2(a)]. *Balistes capriscus* recruited to the commercial longline fishery by age 6 years, the commercial hook-and-line fishery by age 5 years and the recreational fishery by age 4 years. On average, the youngest fish were collected from fishery-independent surveys, with benthic-trawl samples having the youngest mean age (1.8 years), followed by chevron trap (3.5 years) and hook and line samples (3.8 years). Fish recruited to fishery-independent gears by age 1 year for the benthic trawl and age 3 years for chevron trap and hook and line gear [Fig. 2(b)].

TABLE III. Analysis of variance table indicating three-way model results testing effects of age, sex and data source (fishery-independent v. recreational) on ln-transformed *Balistes capriscus* fork length

Source	d.f.	Sum of squares	Mean of squares	<i>F</i>	<i>P</i>
Age	4	7.909	1.977	126.0	<0.001
Sex	1	1.320	1.320	84.1	<0.001
Source	1	4.284	4.284	273.0	<0.001
Age × sex	4	0.107	0.027	1.7	>0.05
Age × source	4	0.138	0.413	2.2	>0.05
Sex × source	1	0.413	0.090	26.3	<0.001
Age × sex × source	4	0.360	0.157	5.7	
Residual	1931	30.300	1734		
Total	1950	57.255			

SIZE AT AGE AND GROWTH

The three-way interaction (age × sex × source) in the ANOVA computed to test the effects of sex and sample source on *B. capriscus* size at age was significant (Table III and Fig. 3). When the three-way interaction was sliced by source, sex was significant for size at age for both fishery-independent (Holm-Sidak $P < 0.001$) and recreational (Holm-Sidak $P < 0.001$) data sources. On average, males were 11.1% larger than females for fishery-independent samples and 3.1% larger than females for recreational samples among the five ages examined (Fig. 3). When the age × sex × source interaction was sliced by sex, there was a significant difference in size at age for both males and females between fishery-independent and recreational data sources (Holm-Sidak $P < 0.001$). On average, recreational samples were 17.3% larger than fishery-independent samples for females and 9.0% larger than fishery-independent samples for males among the five ages examined (Fig. 3).

There was a significant difference between the VBGF model that included juvenile size-at-age data compared with the model that did not [$\chi^2 = 278$, $P < 0.001$; Table IV and Fig. 4(a)]. The growth functions for all ages including the juvenile samples had t_0 estimates that were much closer to the origin ($t_0 = -0.06$) v. the function that did not include juvenile data ($t_0 = -1.47$) (Table IV). Growth functions including juvenile data differed significantly by sex ($\chi^2 = 126$, $P < 0.001$), with males having a larger estimated L_∞ than females (405 v. 387 mm L_F) [Fig. 4(b)]. Estimates of k and t_0 were similar between sexes (Table IV).

DISCUSSION

Results of this study clearly indicate sexually dimorphic growth in *B. capriscus*, but whether samples came from fishery-independent surveys or were landed in the recreational fishery also significantly affected estimates of size at age. Not only was a variety of gear types used to sample or capture *B. capriscus*, but those gears were also deployed in a wide range of depths which probably had some effect on the size and age distributions of samples. Samples of pre-settlement age 0 fish that are typically associated with *Sargassum* (Wells & Rooker, 2004) were captured with neuston nets. These

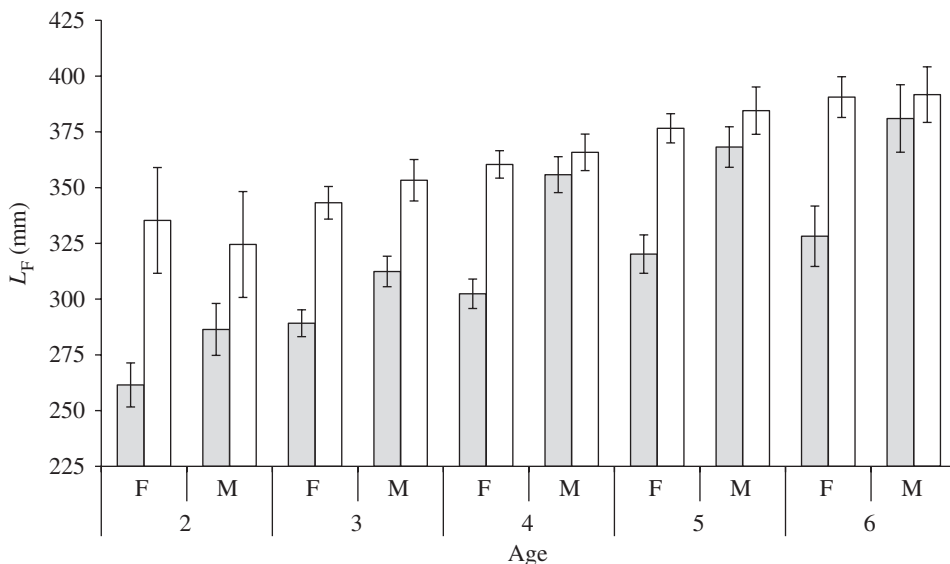


FIG. 3. Mean \pm 95% C.I. sex-specific fork length (L_F) at age for *Balistes capriscus* sampled on fishery-independent surveys (\square) or from recreational landings (\square) in the northern Gulf of Mexico. F, female; M, male.

fish ranged in size from 2.7 to 94 mm L_F and were collected from May to September which is consistent these fish being age 0 juveniles. In addition, these fish were similar in size to *Sargassum* associated *B. capriscus* (13.2–105.8 mm L_S) reported by Wells & Rooker (2004) that were collected from May to August. Benthic trawls, which were only utilized in fishery-independent sampling, collected the smallest, newly settled individuals. Hook and line (both fishery-independent and fishery-dependent) and trap gears (fishery-independent only) sampled intermediate sizes and longline gear (fishery-dependent only) captured the largest fish. This trend in fish size by gear type might be partly due to ontogenetic shifts in habitat, which is clearly true for the transition between neustonic juvenile and early post-settlement stages. Many marine fishes, however, also transition to deeper habitats as they age (Macpherson & Duarte, 1991) and all longline-caught *B. capriscus* samples came from >40 m depth due to fishery regulations. Among fishery-independent samples, 73% of trap sets and 84% of trawls were fished in water <30 m.

Gear selectivity and minimum size limit regulations also probably affected the differences observed in estimates of size at age between fishery-independent and recreational samples. The fact that per cent difference in male v. female L_F was over 3 times greater for recreational samples, supports the inference that selectivity was an important factor in differences in size at age. Data presented here clearly demonstrate that males grow faster than females, thus would recruit to hook-and-line gear, e.g. quicker than females. Therefore, the effect of gear selectivity on estimates of size at age would be greater for slower growing females in that only the fastest growing females would recruit to fishery-dependent gear deploying larger hooks, at young ages.

The influence of gear selectivity on estimates of size at age and growth has important implications for examining the population ecology of *B. capriscus*, as well as for

TABLE IV. von Bertalanffy growth parameters for *Balistes capriscus* from the current study and previous Gulf of Mexico studies

Study	<i>n</i>	Maximum age (years)	L_{∞} (mm)	K (year ⁻¹)	t_0 (years)
Current study					
All observations	4498	14	589	0.17	-1.47
All observations with juveniles	5361	14	484	0.34	-0.06
Males	1766	9	405	0.55	0.02
Females	2324	10	387	0.52	0.004
Johnson & Saloman (1984)					
All observations	2808	13	466	0.38	0.19
Male	1334	9	492	0.38	0.23
Female	1228	12	438	0.38	0.15
Ingram (2001)					
All observations	1625	8	583	0.18	-1.58
Males	781	8	598	0.2	-1.37
Females	814	8	514	0.21	-1.61
P. B. Hood & A. K. Johnson (unpubl. data)					
All observations	626	14	645	0.15	-1.9
Males	307	14	664	0.16	-1.8
Females	143	10	421	0.33	-1.2

integrated stock assessments in which growth is modelled within the assessment model, most often from a sub-sample of landings that has been aged. Most length-at-age data sets collected for growth analysis are from size-selective capture methods that favour fast-growing individuals (Taylor *et al.*, 2005). Overestimating growth on the order of 10% is likely to have a substantial effect on estimates of stock productivity. The most recent assessment of *B. capriscus* was performed with the Stock Synthesis III integrated assessment platform (SEDAR, 2015), thus simulations of overestimating the growth rate should be easy to implement.

Sexually dimorphic growth reported here for *B. capriscus* clearly also has important implications for estimating population dynamics and productivity. Authors of previous studies of GOM *B. capriscus* suggested sexually dimorphic growth existed for this species, but that inference was supported by growth functions that often were poorly fitted given the lack of small, young fish in the data (Johnson & Saloman, 1984; Ingram, 2001; P. B. Hood & A. K. Johnson, unpubl. data). This is reflected in the large, negative t_0 parameters (*i.e.* < -1.0 years) of most of these earlier growth functions, which then also resulted in unreliable estimates of k and L_{∞} and uncertainty about sexually dimorphic growth. Testing differences in size at age by sex in the current study clearly demonstrates that males are larger at age than females. Furthermore, the inclusion of data from age 0 individuals provided a more realistic fit near the origin for the VBGF, resulting in more realistic estimates of t_0 and overall improved fit to the data. Combining age samples from multiple gear types has been shown to reduce bias and increase precision in VBGF estimation (Wilson *et al.*, 2015). The VBGFs reported by Johnson & Saloman (1984) also fit well at the origin, but to do so they had to rely on back-calculated length at age for small, young fish and their estimates of L_{∞} and k were affected by the lack of older fish in their data.

Aspects of *B. capriscus* reproductive biology and behaviour provide insight into why larger male size may convey fitness in this species. Typically, male size is affected

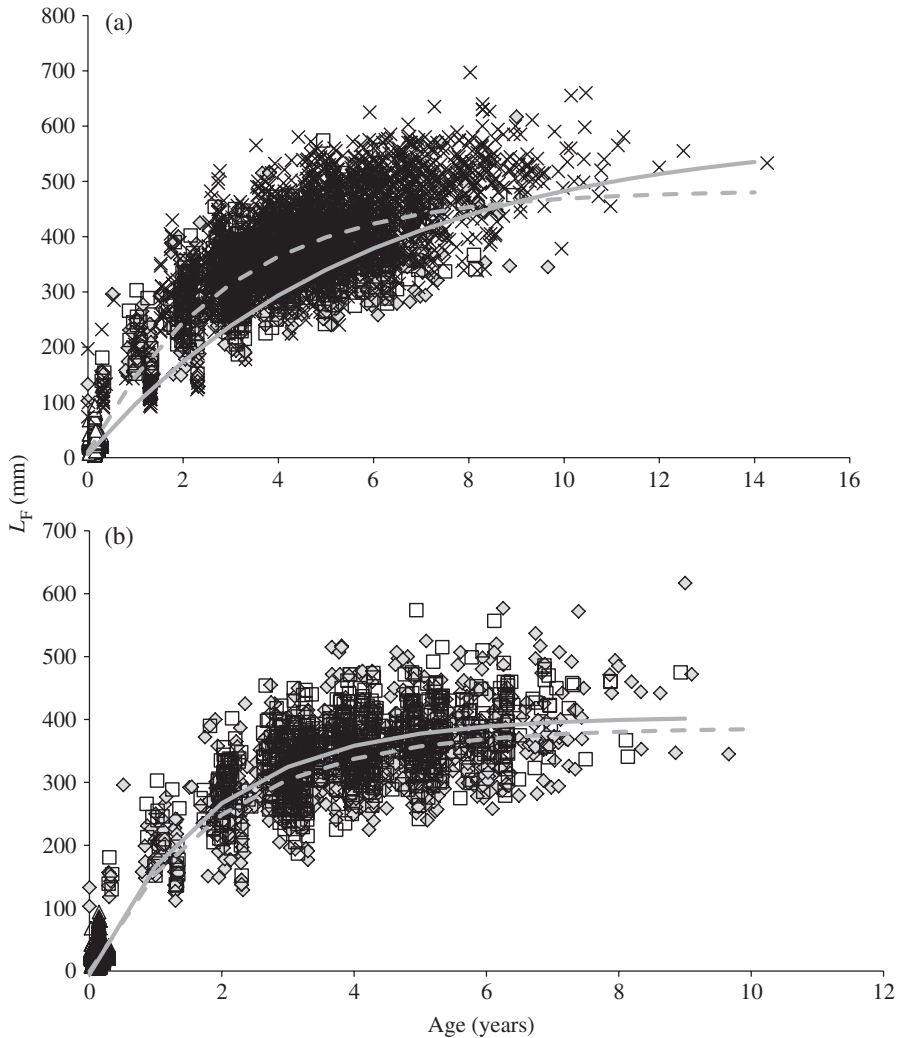


FIG. 4. Fork length (L_F)-at-fractional-age data for *Balistes capriscus* from the Gulf of Mexico 2003 to 2013 with fitted von Bertalanffy growth-function curves for: (a) mature males and females, including unknown sex (—) and with juveniles (---); (b) for males (—), females (---) including juveniles. \diamond , females; \square , males; \triangle , juveniles; X, unknown sex.

by sexual selection in contests for females and spawning opportunities (Parker, 1992) and *B. capriscus* have distinctive reproductive behaviour that is consistent with selection pressure for larger, faster growing males to ensure reproductive success. For example, Simmons & Szedlmayer (2012) reported that male *B. capriscus* exhibit aggressive, territorial behaviour during the spawning season and may guard several females on nests with demersal eggs until hatching. Therefore, not only are larger males more able to compete for territory and females, but larger males also are likely to be more able to effectively guard nests once spawning has occurred. Sex ratios were significantly different than 1:1 favouring females. In contrast to present results, P. B. Hood & A. K. Johnson (unpubl. data) found a ratio of 2:1:1 male to female

for GOM fishery-dependent catches. Kelly-Stormer *et al.* (2017) and J. L. Moore (unpubl. data) found that overall females were dominant in catches of *B. capriscus* from the southern U.S. Atlantic Ocean, but that males outnumbered females in larger size classes (>400 mm L_F). In the present study it was found that females consistently outnumbered males in every size class. A sex ratio favouring females may be a successful reproductive strategy given the life history of *B. capriscus*, with males attracting a harem of females with which to mate (Simmons & Szedlmayer, 2012).

Clearly, any analysis of factors affecting size at age or growth is contingent upon having reliable age estimates. Annual deposition of translucent zones in *B. capriscus* spines has been validated *via* chemical marking (Allman *et al.*, 2016), but difficulty in counting translucent zones in spine sections can lead to inaccurate or imprecise age estimates. The APE reported here between readers of *B. capriscus* spine sections (10.8%) is higher than the 5% threshold commonly utilized to assess ageing reliability in moderately long-lived bony fishes (Morison *et al.*, 1998; Campana, 2001). A difference in counts between readers of even a single translucent zone will however, have a much greater effect on APE for fish that are <10 years old than older fish. For example, a single zone difference in counts for a 5 year-old fish would yield an APE of 20%, while the same one zone difference in a 20 year-old fish would produce an APE of 5%. That said, the greatest contributor to the relatively high APE reported here for *B. capriscus* spines, both for study samples (10.8%) and for samples with accepted age estimates in a reference set (9.1%), is the difficulty in interpreting and counting translucent zones in spine sections. For example, Kelly-Stormer *et al.* (2017) reported an APE of 12% and Burton *et al.* (2015) reported an APE of 11% for *B. capriscus* sampled in the Atlantic Ocean off the south-eastern U.S. In the end, it is assumed that ageing error was randomly distributed among samples and results of hypothesis testing were not affected by systematic bias in ageing.

Overall, results of this study make important contributions to an understanding of *B. capriscus* population dynamics in the GOM. This study provides greater evidence for the efficacy of age estimation based on dorsal spines for *B. capriscus* and perhaps other marine fishes, despite lower between-reader precision than is typical for bony-fish age estimation utilizing otoliths. This has been particularly important for the transition to age-based integrated stock assessment for this species in the GOM which appears to be superior to the surplus production models historically utilized to assess stock status (SEDAR, 2015). Lastly, present findings highlight potential issues, such as sexual dimorphism and effects of fishery selectivity that may bias estimates of size at age and growth if not accounted for in growth analysis. Future work on *B. capriscus* should explore the implications of sexual dimorphism and fishery selectivity on estimates of stock productivity and yield for this important fishery species.

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