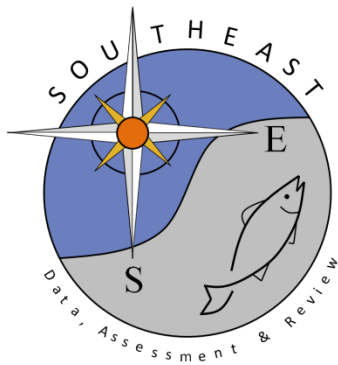


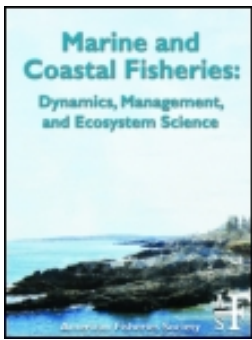
# Age, Growth, and Mortality of Yellowmouth Grouper from the Southeastern United States

Michael L. Burton, Jennifer C. Potts & Daniel R. Carr

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ARTICLE

## Age, Growth, and Mortality of Yellowmouth Grouper from the Southeastern United States

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### Abstract

The Yellowmouth Grouper *Mycteroperca interstitialis* is a member of the snapper–grouper complex that is managed by the South Atlantic Fishery Management Council. There is little published life history information—specifically age–growth parameters—for use in assessing the resource. We sampled Yellowmouth Grouper from the fisheries along the southeastern U.S. coast from 1980 to 2012 ( $n = 391$ ), determining ages by counting opaque zones on sectioned sagittal otoliths. Opaque zones were annular, forming in May–August with a peak in May and June. Yellowmouth Grouper age ranged from 3 to 31 years, and the largest fish was 859 mm FL. Body size relationships were as follows: whole weight  $W$  (g) =  $(8.89 \times 10^{-6})(\text{FL, mm})^{3.07}$  ( $n = 339$ ;  $r^2 = 0.96$ );  $W$  (g) =  $(1.13 \times 10^{-5})(\text{TL, mm})^{3.01}$  ( $n = 165$ ;  $r^2 = 0.96$ ); and TL (mm) =  $10.09 + [1.05 \times (\text{FL, mm})]$  ( $n = 162$ ;  $r^2 = 0.98$ ). The von Bertalanffy growth equation for Yellowmouth Grouper was  $L_t$  (length at age  $t$ ) =  $755[1 - e^{-0.14(t + 1.42)}]$  when the model included an adjustment for minimum size limits and was  $L_t = 772[1 - e^{-0.11(t + 4.18)}]$  when the model was not adjusted. Natural mortality ( $M$ ) estimated by Hewitt and Hoenig's (2005) longevity-based method was 0.14. Age-specific estimates of  $M$  were obtained with the Charnov et al. (2013) method. The selection of growth model (size limit adjusted versus unadjusted) had a marked effect on  $M$  for the earliest ages:  $M$  was 1.22 versus 0.43 for age 0; 0.72 versus 0.35 for age 1; 0.51 versus 0.29 for age 2; 0.40 versus 0.26 for age 3; 0.33 versus 0.23 for age 4; and 0.29 versus 0.21 for age 5. We believe that these life history parameter estimates are accurate for Yellowmouth Grouper in southeastern U.S. fisheries.

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The Yellowmouth Grouper *Mycteroperca interstitialis* (family Serranidae) is widely distributed throughout the western Atlantic Ocean. The species occurs throughout the southeastern USA (SEUS) from North Carolina through the Florida Keys and into the Gulf of Mexico and is also found in the waters off Bermuda and the Bahamas (Smith 1971). Its range further extends through the Caribbean Sea south to Brazil (Smith 1978). Yellowmouth Grouper are present in subtropical and temperate hard-bottom areas to depths of 150 m (Heemstra and Randall 1993) but are most commonly found at depths of 2–35 m (Bullock and Smith 1991; Gaspirini and Floeter 2001).

Bullock and Murphy (1994) observed that the Yellowmouth Grouper is physically similar in appearance to its congener, the Scamp *Mycteroperca phenax*. This visual similarity has caused

misidentification of Yellowmouth Grouper as Scamps and has led to uncertainty in the commercial and recreational landings data for Scamps, although the exact magnitude of misidentification is unknown. Bullock and Murphy (1994) posited that the Yellowmouth Grouper contribution to Scamp landings was low.

Yellowmouth Grouper are of moderate importance to the SEUS fishery for reef fish. Estimated annual landings from headboats sampled by the Southeast Region Headboat Survey (SRHS) averaged 292 kg between 1986 and 2010 (K. J. Brennan, National Marine Fisheries Service [NMFS], unpublished data). These landings equate to an average ranking of 45th among the 73 species that are managed by the South Atlantic Fishery Management Council (SAFMC) under the Snapper–Grouper Fishery Management Plan. Estimated landings from private recreational

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boats and charter boats (T. Sminkey, NMFS, unpublished data) averaged 950 kg annually from 1988 to 2007. Commercial fisheries of the SEUS (D. Gloeckner, NMFS, Southeast Fisheries Science Center, unpublished data) harvested a total of 1,042 kg of Yellowmouth Grouper from 1991 to 2011. Landings are widely distributed along the U.S. east coast from North Carolina through the Florida Keys, including the Dry Tortugas. Although landings of Yellowmouth Grouper are relatively low in all three fishery sectors, the Yellowmouth Grouper, like the Scamp, is valued for its large size, fighting ability, and food value.

The SAFMC (SAFMC 2013) currently manages Yellowmouth Grouper with a 508-mm (20-in) TL size limit, which was enacted in 1992 for both the commercial and recreational fisheries. Furthermore, since 2012, Yellowmouth Grouper have been included in (1) a shallow-water grouper closed season each year from January 1 to April 30 for both fishery sectors and (2) an aggregate 3-grouper-person<sup>-1</sup>.d<sup>-1</sup> bag limit for recreational fishers outside of the closed season (a 5-grouper bag limit was in effect from 1992 to 2011).

Published studies on Yellowmouth Grouper life history characteristics that are relevant to fishery managers have exclusively focused on the Gulf of Mexico and Caribbean populations. Observations on the reproductive biology, food habits, and parasites of specimens captured from the Florida Middle Grounds in the Gulf of Mexico were reported by Bullock and Smith (1991). Smith (1971) documented spawning of Yellowmouth Grouper in Bermuda, and Thompson and Munro (1978) documented fish in spawning condition from Jamaican waters. Randall (1967) described food habits of specimens from the Bahamas. Bullock and Murphy (1994) described reproduction, growth, and mortality of Yellowmouth Grouper from the eastern Gulf of Mexico. Manickchand-Heileman and Phillip (2000) described age and growth of the species from Trinidad and Tobago.

We studied Yellowmouth Grouper from the SEUS because little is known of their life history parameters despite the fact that these parameters are important as input variables for single-species, multispecies, or ecosystem-based modeling efforts, either as stand-alone species data or in defining more inclusive functional groups of species (Christensen et al. 2009). For species managed under the SAFMC Snapper-Grouper Fishery Management Plan that are relatively uncommon in the landings and for which little life history data are available, the SAFMC has explored the possibility of using congeners as management proxies. The Scamp is a possible proxy for Yellowmouth Grouper due to these species' close resemblance. In the present paper, we provide information on life history parameters for Yellowmouth Grouper sampled from SEUS waters, compare the life history parameters with those of Yellowmouth Grouper studied in other areas, and explore whether the parameters are similar to those of Scamps.

## METHODS

*Age determination and validation of annuli.*—Yellowmouth Grouper were opportunistically sampled from fisheries landings

along the SEUS coast from 1980 to 2012. All specimens were captured by either conventional vertical hook-and-line gear or longline gear. Sagittal otoliths were collected from 391 Yellowmouth Grouper by NMFS port agents sampling the recreational headboat and commercial fisheries. Lengths (FL, TL, or both) of specimens were recorded in millimeters. Whole weight ( $W$ ) was recorded for fish landed in the headboat fishery. Fish that were landed by commercial fisheries were eviscerated at sea; thus, data on  $W$  for those samples were not available. Otoliths were removed during at-sea or dockside sampling and were stored dry in coin envelopes. The majority of sampling occurred at the docks; thus, it was not possible to obtain exact catch locations or depths. Otoliths were sectioned with a low-speed saw by following the methods of Potts and Manooch (1995). Three serial 0.5-mm sections were taken near the otolith core. The sections were mounted on microscope slides with thermal cement and were covered with mounting medium before analysis. The sections were viewed under a dissecting microscope at 12.5 × magnification using reflected light. Each sample was assigned an opaque zone count (ring count) by a single reader (M.L.B.) with extensive experience in the interpretation of otolith sections (Stiles and Burton 1994; Burton 2001, 2002; Burton et al. 2012). In most cases, a single viewing was enough to assign a count, but more difficult sections were set aside and viewed again later for a final determination.

Increment periodicity was assessed using edge analysis. The edge type of the otolith was noted (1 = opaque zone forming on the edge of the otolith section; 2 = narrow translucent zone on the edge, generally < 30% of the width of the previous translucent zone; 3 = moderate translucent zone on the edge, generally 30–60% of the width of the previous translucent zone; 4 = wide translucent zone on the edge, generally > 60% of the width of the previous translucent zone; Harris et al. 2007). Based upon edge frequency analysis, all samples were assigned a chronological (calendar) age, which was obtained by increasing the opaque zone count by 1 if the fish was caught before that year's increment was formed and had an edge consisting of a moderate to wide translucent zone (edge type 3 or 4). Fish that were caught during the period of opaque zone formation with an edge type of 1 or 2 were assigned a calendar age equal to the opaque zone count. All fish that were caught after opaque zone formation had a chronological age equivalent to the opaque zone count.

*Growth.*—We employed the multimodel inference (MMI) approach of Katsanevakis and Maravelias (2008) to determine the most appropriate of three commonly used growth models: the von Bertalanffy (1938) model, the Gompertz (1825) model, and the logistic model (Ricker 1975). The MMI approach utilizes Akaike's information criterion (AIC; Akaike 1973). We estimated growth parameters from the observed length-at-age data by using the nonlinear least-squares (nls) estimation package in R (R Development Core Team 2012), with the analysis adapted from the fishmethods package for R (Nelson 2013). The process of maximizing the likelihood involves calculating the  $n \times p$  gradient matrix ( $n$  = sample size;  $p$  =

number of parameters). By default, the nls package computes the gradient numerically with a finite difference approximation. We estimated the AIC values as

$$\text{AIC} = n \cdot \log_e (\text{RSS}/n) + (2 \times p),$$

where RSS is the residual sum of squares (SAS Institute 1987). Additionally, we estimated the von Bertalanffy growth parameters by using the size-modified model of McGarvey and Fowler (2002), which assumes a left-truncated normal distribution of lengths at age; this was done to account for the effect of nonrandom sampling due to minimum size limits (i.e., the recreational and commercial size limit of 508 mm [20 in] FL beginning in 1992). The McGarvey and Fowler (2002) model estimates parameters by minimizing the negative sum of the log-likelihoods, assuming constant SDs for size at age.

The age of the fish was adjusted for the time of year in which the fish was caught ( $\text{Mo}_c$ ), thus creating a fractional age ( $\text{Age}_f$ ) from the chronological age ( $\text{Age}_c$ ) based on a May birthdate ( $\text{Mo}_b$ ):

$$\text{Age}_f = \text{Age}_c + [(\text{Mo}_c - \text{Mo}_b) / 12].$$

This birthdate was selected based on reproductive studies showing that the peak spawning of Yellowmouth Grouper occurs during April–May in the Gulf of Mexico (Bullock and Smith 1991) and that the peak spawning of Scamps occurs during May–June in the waters off North Carolina and South Carolina (Matheson et al. 1986).

**Body size relationships.**—We regressed  $W$  (g) on FL (mm) and TL (mm) of Yellowmouth Grouper sampled by the SRHS from 1972 to 2010 ( $n = 339$ ). We also regressed TL on FL ( $n = 165$ ) by using the SRHS data set. For all relationships, we examined both a nonlinear fit by using nonlinear least-squares estimation (SAS Institute 1987) and a linearized fit of the log-transformed data; we then examined the residuals to determine which regression was appropriate.

**Natural mortality.**—We estimated the instantaneous rate of natural mortality ( $M$ ) by using two methods. Hewitt and Hoening's (2005) longevity-based relationship was

$$M = 4.22/t_{max},$$

where  $t_{max}$  is the maximum age of fish in the sample. Charnov et al.'s (2013) estimation method based on life history parameters was

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

where  $L_\infty$  is asymptotic length from the von Bertalanffy growth equation,  $K$  is the Brody growth coefficient from the von Bertalanffy equation, and  $L$  is fish length at age. The Hewitt and Hoening (2005) method uses life span or longevity to generate a single point estimate and is an improvement over the

original equation of Hoening (1983). The newer Charnov et al. (2013) method, which incorporates life history information via the growth parameters, is based upon evidence suggesting that  $M$  decreases as a power function of body size. This latter method generates age-specific rates of  $M$  and is currently used in the Southeast Data Assessment and Review stock assessments (E. Williams, NMFS, Beaufort Laboratory, Beaufort, North Carolina, personal communication).

## RESULTS

### Age Determination and Validation of Annuli

In total, 391 sagittal otoliths of Yellowmouth Grouper were sectioned. The distribution (by area and fishery sector) of samples available for age analysis is shown in Table 1. The majority of samples came from the North Carolina and South Carolina commercial fishery sector. Approximately 10% of otolith samples were from Florida collections, the majority of which were obtained from the headboat sector. Opaque zones were counted on 388 (99%) of the 391 sectioned otoliths. Sections from three otoliths were unreadable and therefore excluded from the study.

We were able to assign an edge type to all 388 samples for our analysis of increment periodicity. Opaque zones on

TABLE 1. Number of otolith samples available for use in the age–growth study of Yellowmouth Grouper from the southeastern USA. One additional sample was collected off Florida's east coast by a private recreational fishing boat.

Year	Commercial fishery		Headboat fishery		
	North Florida	South Carolina	North Carolina	South Carolina	Carolina
1980				10	
1981				9	
1982				1	
1983				6	1
1984				1	
1989					3
1993				1	
1996				1	13
1997	2			2	2
1999	4				
2001	1				
2002					1
2004		5		1	
2005		32	1		
2006		9	53		
2007		58	14		
2008		17	13	3	
2009		13	20	1	1
2010		12	10	1	
2011		8	17		
2012		14	16		

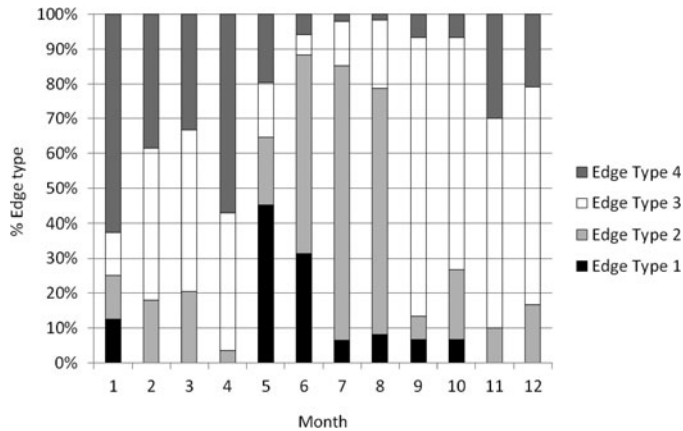


FIGURE 1. Monthly percentages of Yellowmouth Grouper otoliths ( $n = 388$ ) exhibiting the four edge types (1 = opaque zone on edge; 2 = narrow translucent zone, <30% of previous increment; 3 = moderate translucent zone, 30–60% of previous increment; 4 = wide translucent zone, >60% of previous increment).

the otolith marginal edge occurred in samples collected during May–October (Figure 1), although the occurrence of opaque zones on the edge in September and October samples was attributable to a single fish in each month. Thus, we concluded that opaque zone formation occurred during May–August, with most opaque zones being laid down in May and June. Otoliths were without an opaque zone on the edge during November–April, with the exception of one January sample that exhibited an opaque zone. The least amount of translucent edge occurred during May–August, whereas the width of the translucent edge increased later in the year, remaining highest during September–April. We concluded that the opaque zones on Yellowmouth Grouper otoliths were annuli.

All fish were assigned a chronological age for further analyses. The majority of fish had completed their opaque zone formation by the end of June. A shift to a narrow translucent edge was noted in July. Thus, for fish caught in January–June and having an otolith edge type of 3 or 4, the annulus count was increased by 1. For fish caught during that same time period but with an edge type of 1 or 2, the chronological age was equivalent to the annulus count. For fish that were caught during July–December, the chronological age was equivalent to the annulus count.

### Growth

Yellowmouth Grouper in this study ranged in size from 300 to 859 mm FL and ranged in age from 3 to 31 years, but only six fish were older than age 21 (Table 2). Length and age distributions of our aged samples (by fishery sector: commercial versus recreational) are shown in Figures 2a and 3a. Initial visual examination of size and age frequency plots revealed apparent differences in both distributions by fishery sector. Further analysis revealed that these differences were driven by recreational samples collected before 1992, when the 508-mm (20-in) size limit went into effect. Visual examination of the length and age fre-

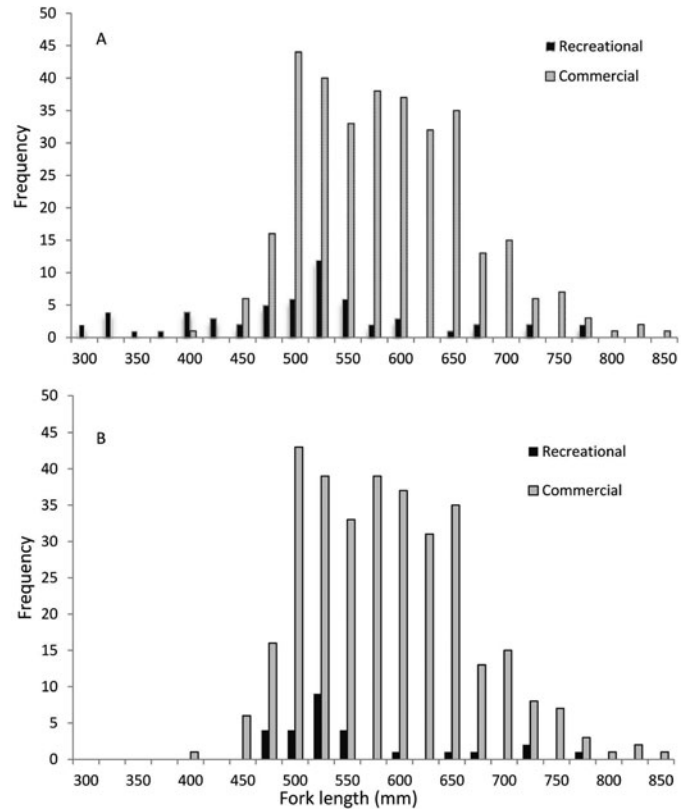


FIGURE 2. Length frequencies of Yellowmouth Grouper (used in otolith age determination) collected from the recreational and commercial fishery sectors in the southeastern USA during (A) 1980–2012 and (B) 1992–2012.

quency data for only the years 1992–2012 (Figures 2b, 3b) found no differences between the FL modes of Yellowmouth Grouper obtained from the two sectors (500 mm FL for the commercial sector versus 525 mm FL for the recreational sector; Figure 2b). Average FLs of the specimens were not significantly different between the two fishery sectors (commercial [mean  $\pm$  SE]:  $598 \pm 4.3$  mm FL; recreational:  $565 \pm 15.9$  mm FL;  $t = -1.98$ ,  $df = 26$ ,  $P = 0.06$ ). The modal age was 7 years for fish from the commercial sector and 6 years for fish from the recreational sector (Figure 3b). Mean age was not significantly different between sectors (commercial [mean  $\pm$  SE]:  $9.8 \pm 0.24$  years; recreational:  $8.4 \pm 0.81$  years;  $t = 1.65$ ,  $df = 26$ ,  $P = 0.11$ ). Analysis of the covariance of length at age by fishery sector with age as the covariate found no significant differences between the sectors ( $P = 0.33$ ). Based on these results, we pooled data across the two sectors.

The MMI approach revealed that the von Bertalanffy growth model was the most appropriate as measured by the AIC method, although all three models had a similar fit to the data (AIC = 2,792.401 for the von Bertalanffy model; 2,792.795 for the Gompertz model; and 2,793.981 for the logistic model). The resulting von Bertalanffy growth equation was

$$L_t = 772[1 - e^{-0.11(t+4.18)}]$$

TABLE 2. Observed FL at age and FL range for Yellowmouth Grouper from the southeastern USA; predicted FL (mm) from three von Bertalanffy growth models (a size-limit-corrected model with  $t_0$  [theoretical age at a length of zero] constrained to 0; a size-limit-corrected model with unconstrained  $t_0$ ; and a model without a correction for size limits); and natural mortality ( $M$ ) at age estimated by the Charnov et al. (2013) method using the three growth models. Natural mortality was calculated from the midpoint of each age (age 0.5, 1.5, 2.5, etc.).

Age	$n$	Mean FL (mm) $\pm$ SE	FL range (mm)	Predicted FL (mm)			$M$		
				Size limit correction and $t_0 = 0$	Size limit correction	Uncorrected	Size limit correction and $t_0 = 0$	Size limit correction	Uncorrected
0				0	137	291	7.04	1.22	0.42
1				122	218	342	1.55	0.72	0.34
2				223	289	388	0.82	0.51	0.29
3	4	422 $\pm$ 46	336–510	307	350	429	0.56	0.4	0.25
4	15	424 $\pm$ 24	300–642	377	403	466	0.44	0.33	0.23
5	25	496 $\pm$ 8	404–592	435	450	498	0.36	0.29	0.21
6	44	539 $\pm$ 7	430–660	483	490	528	0.32	0.26	0.19
7	63	548 $\pm$ 5	438–641	523	525	554	0.28	0.23	0.18
8	41	563 $\pm$ 9	400–670	556	555	577	0.26	0.22	0.17
9	39	590 $\pm$ 9	500–700	584	581	598	0.25	0.2	0.16
10	26	599 $\pm$ 13	500–760	607	604	617	0.23	0.19	0.15
11	31	624 $\pm$ 10	520–750	626	624	633	0.22	0.18	0.15
12	27	632 $\pm$ 11	490–730	642	641	648	0.22	0.18	0.14
13	19	647 $\pm$ 16	550–859	655	656	661	0.21	0.17	0.14
14	8	668 $\pm$ 29	540–840	666	669	673	0.21	0.17	0.14
15	9	700 $\pm$ 13	650–760	675	680	684	0.20	0.16	0.13
16	11	707 $\pm$ 21	620–830	683	690	693	0.20	0.16	0.13
17	7	677 $\pm$ 21	580–740	689	699	701	0.20	0.16	0.13
18	2	775 $\pm$ 6	769–780	694	706	709	0.19	0.15	0.13
19	4	748 $\pm$ 26	685–800	699	713	716	0.19	0.15	0.13
20	3	718 $\pm$ 40	660–795	702	718	722	0.19	0.15	0.12
21	4	718 $\pm$ 9	690–730	705	723	727	0.19	0.15	0.12
22	1	690		708	727	732	0.19	0.15	0.12
23				710	731	736	0.19	0.15	0.12
24	1	760		712	734	740	0.19	0.15	0.12
25	2	718 $\pm$ 18	700–736	713	737	743	0.19	0.15	0.12
26				714	739	747	0.19	0.15	0.12
27				715	741	749	0.19	0.14	0.12
28	1	720		716	743	752	0.19	0.14	0.12
29							0.19	0.14	0.12
30							0.19	0.14	0.12
31	1	770		718	747	758	0.19	0.14	0.12

( $n = 388$ ; Table 3; Figure 4), where  $L_t$  is length at age  $t$ . Because our data included no fish below age 3, the model was not able to capture initial growth of fish at ages 0, 1, and 2, thus explaining the large negative value of  $t_0$  (theoretical age at a length of zero). The lack of smaller fish is probably explained by gear selectivity, as our samples were all fishery dependent; the problem was likely exacerbated by the enactment of the 508-mm (20-in) size limit in 1992, which prevented us from sampling smaller fish. We thus re-ran the growth model using the method of McGarvey and Fowler (2002), which adjusts

for the bias imposed by minimum size limits by assuming a zero probability of capture below the minimum size limit. The resulting von Bertalanffy growth equation was

$$L_t = 755[1 - e^{-0.14(t+1.42)}].$$

### Body Size Relationships

Statistical analyses revealed a multiplicative error term (variance increasing with size) in the residuals of the  $W$ -FL and

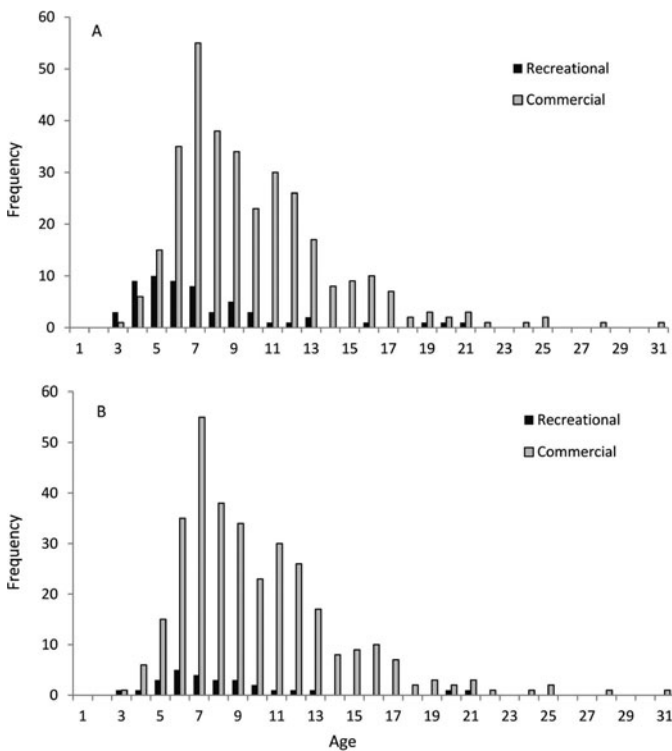


FIGURE 3. Age distribution of Yellowmouth Grouper (used in otolith age determination) collected from the recreational and commercial fishery sectors in the southeastern USA during (A) 1980–2012 and (B) 1992–2012.

$W$ – $TL$  relationships for Yellowmouth Grouper, indicating that a linearized  $\log_e$  transform fit of the data was appropriate. The relationships are described by the following regressions:

$$\log_e(W) = 3.01 \cdot \log_e(TL) - 11.39$$

( $n = 165$ ;  $r^2 = 0.96$ ) and

$$\log_e(W) = 3.07 \cdot \log_e(FL) - 11.63$$

TABLE 3. Comparison of von Bertalanffy parameters ( $L_\infty$  = asymptotic length;  $K$  = Brody growth coefficient;  $t_0$  = theoretical age at a length of zero) from various studies of Yellowmouth Grouper (YMG) and Scamps (one study); the peak period of opaque otolith edge observations, peak spawning period, and parameters of the length–weight ( $L$ – $W$ ) equation ( $a$  = intercept;  $b$  = slope) are also shown.

Species (data source)	$L_\infty$	$K$	$t_0$	Peak period of opaque edge in otoliths	Peak spawning period	$L$ – $W$ : $a$	$L$ – $W$ : $b$
YMG, U.S. Gulf of Mexico (Bullock and Murphy 1994)	828 mm TL; 800 mm FL	0.08	–7.5	Aug–Oct	Apr–May	$2.58 \times 10^{-8}$	2.89
YMG, Trinidad and Tobago (Manickchand-Heileman and Phillip 2000)	854 mm FL	0.06	–4.6	Sep–Jan	Apr–Jul	$1.88 \times 10^{-8}$	2.94
Scamp, U.S. South Atlantic (Matheson et al. 1986)	985 mm FL	0.09	–2.45	Dec–Apr	May–Jun	$2.4 \times 10^{-8}$	2.91
YMG (this study)	755 mm FL	0.14	–1.42	May–Jun		$8.89 \times 10^{-6}$	3.07

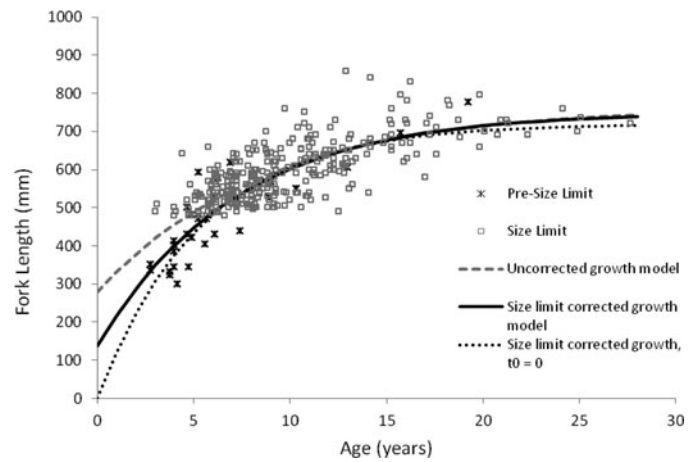


FIGURE 4. Comparison of mean observed size at age (years) and sizes predicted by three von Bertalanffy growth models (a size-limit-corrected model with  $t_0$  [theoretical age at a length of zero] constrained to 0; a size-limit-corrected model with unconstrained  $t_0$ ; and a model without a correction for size limits) for Yellowmouth Grouper in the southeastern USA. Pre-size-limit data were collected before implementation of the 508-mm (20-in) minimum length limit in 1992.

( $n = 339$ ;  $r^2 = 0.96$ ). These equations were transformed back to the form  $W = a(L)^b$  after adjusting the intercept for log-transformation bias with the addition of one-half of the mean square error (Beauchamp and Olson 1973). Scatter plots of the data and regression equations are shown in Figure 5. The relationship between  $TL$  and  $FL$  is described by the equation

$$TL = 10.09 + (1.05 \times FL)$$

( $n = 162$ ;  $r^2 = 0.98$ ).

### Natural Mortality

Using Hewitt and Hoenig's (2005) estimation method (i.e., integrating all ages into a single point estimate),  $M$  was estimated at 0.14 based on the maximum age observed in fish



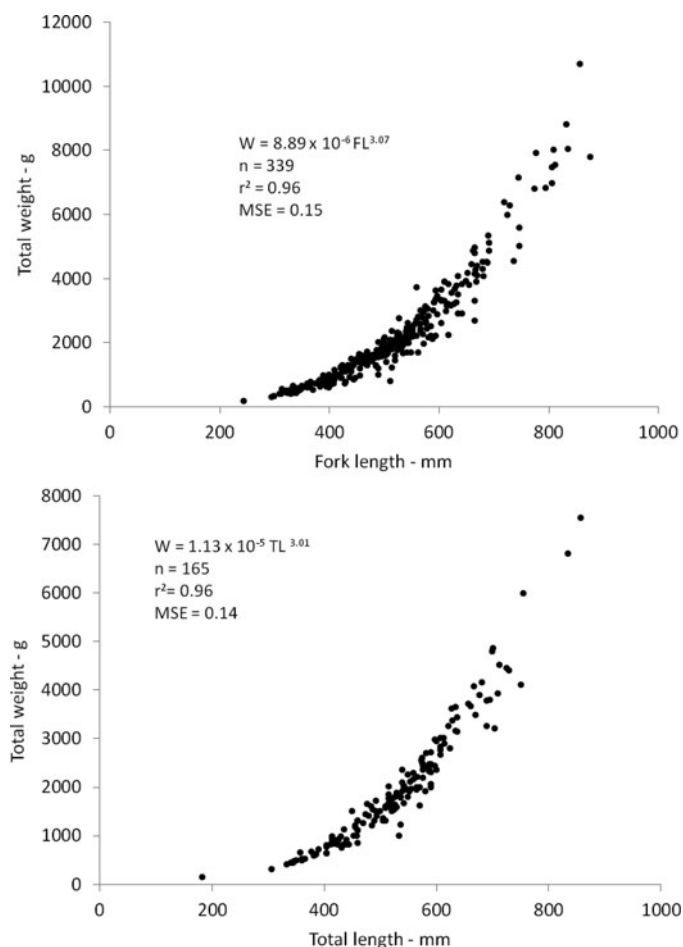


FIGURE 5. Scatter plots of weight-length relationships for Yellowmouth Grouper from the southeastern USA ( $W$  = weight; MSE = mean square error).

from our study (31 years). Because the Charnov et al. (2013) age-specific calculation of  $M$  assumed a von Bertalanffy growth function with  $t_0$  equal to 0, we re-estimated  $K$  and  $L_\infty$  with the constraint of  $t_0 = 0$ . The resulting parameter values were 720.20 mm FL for  $L_\infty$  and 0.185 for  $K$  (Figure 4). Age-specific  $M$ -values estimated using the method of Charnov et al. (2013) for minimum-size-limit-corrected growth parameters (either with  $t_0$  unconstrained or with  $t_0 = 0$ ) and for uncorrected parameters are presented in Table 2. We used the midpoint of each age (e.g., 0.5, 1.5, 2.5, etc.) to calculate age-specific  $M$  because the Charnov et al. (2013) method cannot mathematically calculate  $M$  for age 0. Furthermore, for stock assessment purposes wherein the integer age is used to describe the entire year of the fish's life, the midpoint gives the median value of  $M$  for that age.

## DISCUSSION

One limitation of this study was the lack of Yellowmouth Grouper in smaller size-classes, initially due to the fishery-dependent nature of our samples and the selectivity of the fishing

gear. This limitation was then exacerbated by enactment of the minimum size limit in 1992. These issues are supported by the fact that the youngest fish in our study was age 3. Similarly, Bullock and Murphy (1994) only had three age-2 fish in their study utilizing samples obtained from recreational hook-and-line fishing, and the youngest fish in the study by Manickchand-Heileman and Phillip (2000) was age 5, as collected from the commercial fishery. This lack of young fish, which is common to studies dominated by fishery-dependent samples, can lead to problems in estimating the growth curve for the youngest ages. No data from younger fish exist to help define the trajectory of the growth curve at the earliest ages, so this area of the growth curve should be interpreted with caution. We accounted for this problem by correcting our growth model analysis for the minimum size limit via McGarvey and Fowler's (2002) method, which uses a truncated likelihood to alleviate the overestimation bias in mean lengths at age resulting from specimens being restricted to larger sizes by a minimum size limit. This technique had a slight effect on estimates of  $L_\infty$  and  $K$ , whereas it had a major influence on the estimation of  $t_0$ , reducing  $t_0$  from a value of  $-4.18$  to a more realistic estimate of  $-1.42$ . Given the results of the two methods for estimating the von Bertalanffy growth parameters, we recommend the use of the McGarvey and Fowler (2002) method whenever age samples are obtained from a fishery with minimum size limit regulations in place. Another limitation of our study was the long time period over which samples were collected ( $>30$  years). Population parameters can vary interannually for various reasons (e.g., variable recruitment and environmental conditions), and it is likely that parameter estimates based on samples collected over a 30-year period would show increased variability. Samples from species like the Yellowmouth Grouper and other infrequently caught reef fishes will probably never be obtained in quantities large enough to allow this source of error to be eliminated from the parameter estimates. We need to recognize that these estimates, while currently the best we can generate, are variable.

Due to survey sampling protocols existing at the time of specimen collection, reproductive data were not recorded from the Yellowmouth Grouper used in this study. Published literature shows that Yellowmouth Grouper in the Gulf of Mexico mature between 2 and 4 years of age, corresponding to a size of between 400 and 450 mm TL (Bullock and Murphy 1994). The youngest mature female from the Bullock and Murphy (1994) study was age 2, and that individual measured 420 mm TL. The smallest mature male in their study was 505 mm TL and age 4. Transitional fish (i.e., those undergoing sex change from female to male) were between 505 and 643 mm TL and ranged in age from 5 to 14 years. Scamps from the Gulf of Mexico are also known to be mature at approximately this size; Bullock and Smith (1991) found a 411-mm specimen with hydrated oocytes in samples from the Florida Middle Ground. Matheson et al. (1986) recorded the spawning season for Scamps in North Carolina and South Carolina, but they did not include observations of size or age at maturity. Recognizing the value of age-at-maturity data

as a demographic parameter for inputting into stock assessments, the NMFS Southeast Fisheries Science Center initiated a fishery-independent survey in 2010 (Southeast Fishery Independent Survey) to obtain these data for managed species.

Otolith edge analysis demonstrated that Yellowmouth Grouper deposited one annulus per year from May to August and that peak annulus formation occurred in May and June. Bullock and Murphy (1994) reported that peak annulus formation in Gulf of Mexico Yellowmouth Grouper occurred over a 4-month period (July–October). Manickchand-Heileman and Phillip (2000) found that Yellowmouth Grouper in Trinidad and Tobago deposited annuli from September to January. Scamps sampled from the SEUS deposited annuli from December to April (Matheson et al. 1986). Manickchand-Heileman and Phillip (2000) observed that annulus formation in Yellowmouth Grouper from Trinidad and Tobago occurred after the peak spawning period (Table 3). This would seem to be true for Yellowmouth Grouper in the Gulf of Mexico; otolith deposition began occurring in July after a peak spawning period in April and May. If we use the Gulf of Mexico spawning period as a proxy for Yellowmouth Grouper from the SEUS, the result is similar, although it appears that less time expires before opaque zone deposition begins in SEUS Yellowmouth Grouper relative to individuals from the Gulf of Mexico population or the Trinidad and Tobago population.

Body size relationships were similar between Yellowmouth Grouper from the SEUS and those from the Gulf of Mexico. Length–weight regressions were essentially identical (Table 3). The TL–FL relationships were also similar:  $TL = 10.09 + (1.05 \times FL)$  for Atlantic coast fish versus  $TL = 1.01 + (1.03 \times FL)$  for the Gulf of Mexico population (Bullock and Murphy 1994). When comparing calculated TLs for a given FL, the SEUS equation returns TL values that are, on average, 17 mm larger than those from the Gulf of Mexico equation.

Yellowmouth Grouper in the SEUS grew moderately fast, attaining an average observed size of 422 mm FL by age 3 (Table 2). Bullock and Murphy (1994) found that Yellowmouth Grouper from the Gulf of Mexico grew rapidly, attaining an average observed size of 415 mm by age 2, before growth slowed to approximately 25 mm/year. Growth of fish in our study slowed after age 3, reaching 496 mm by age 5 and then averaging annual size increment increases of 21 mm through age 10. Observed sizes at age 6 and older were similar between our study and the Gulf of Mexico study, with an average difference of 15 mm from age 6 through age 13. Observed sizes at age of the closely related Scamp from the SEUS (Matheson et al. 1986) were similar to those of Yellowmouth Grouper from our study up to age 5 (age 3: 425 mm for Scamps versus 422 mm for Yellowmouth Grouper; age 5: 525 mm for Scamps versus 496 mm for Yellowmouth Grouper). However, Scamps grew faster at older ages, averaging 71 mm larger than Yellowmouth Grouper at ages 6–15. These trends are reinforced by examination of the predicted growth curves for Yellowmouth Grouper (Figure 6), which indicate markedly different growth among studies for the

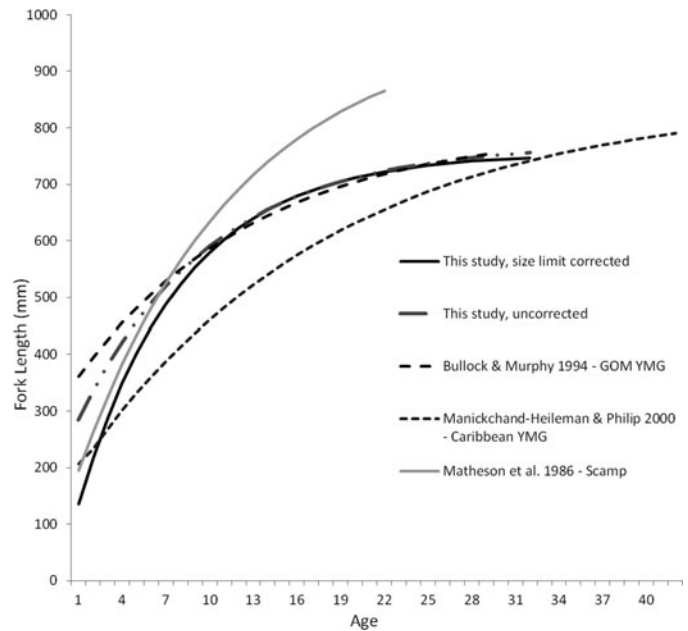


FIGURE 6. Comparison of uncorrected and size-limit-corrected von Bertalanffy growth curves for Yellowmouth Grouper (YMG) from this study and growth curves for YMG and Scamps from previously published studies (GOM = Gulf of Mexico).

earlier ages. After age 10, both the corrected and uncorrected curves from the current study are very similar to the curve from the Gulf of Mexico study (Bullock and Murphy 1994). The differences in the earlier ages are likely due to the lack of younger fish in the samples for both the uncorrected curve and the Gulf of Mexico curve, whereas the correction procedure accounted for that sample deficit in estimating growth at the younger ages. The corrected curve for Yellowmouth Grouper from the current study also exhibits a growth trajectory similar to that of the Scamp curve until age 6, although Scamps are larger than Yellowmouth Grouper at all ages. Scamps then grow at a much faster rate beginning at age 6, thereby attaining a much larger overall maximum size and at a younger age than Yellowmouth Grouper. This trend in the predicted growth curves is the same as that seen in the observed sizes at age.

The predicted growth curve that was estimated using the size-limit-corrected parameters fit the observed data well (Figure 4). The corrected and uncorrected growth curves were identical after age 10, differing only in the earlier ages because the lack of fish younger than age 3 selected into the fishery hindered the adequate modeling of growth at a population level. Yellowmouth Grouper from the Trinidad and Tobago study (Manickchand-Heileman and Phillip 2000) grew slower than fish from any of the other three studies. The theoretical maximum size ( $L_{\infty}$ ) estimated for Yellowmouth Grouper in our study (755 FL mm) was lower than those calculated for Gulf of Mexico fish (828 TL mm [ $\sim 800$  mm FL]; Bullock and Murphy 1994) and Trinidad and Tobago fish (854 mm FL; Table 3). The parameter  $K$ , which estimates the rate at which maximum size is attained, was highest

in our study ( $K = 0.14$ ) relative to 0.08 for Gulf of Mexico fish and 0.06 for the tropical population. Maximum observed age of fish from our study was 31 years, similar to the maximum age of 28 years for Yellowmouth Grouper in the Gulf of Mexico but markedly less than the maximum age of 41 years observed for fish in Trinidad and Tobago.

We find it interesting that the Trinidad and Tobago population (Manickchand-Heileman and Phillip 2000) had the largest  $L_\infty$  observed among the three Yellowmouth Grouper studies, the lowest rate of attainment of that size (i.e.,  $K$ ), and the greatest observed age. The usual expectation is that tropical populations grow faster and reach smaller maximum sizes and ages than subtropical or temperate populations (Longhurst and Pauly 1987; Berrigan and Charnov 1994). However, Manickchand-Heileman and Phillip (2000) pointed out that the Gulf of Mexico population has been exploited for a much longer period than the Trinidad and Tobago population, and thus the Gulf of Mexico fish likely exhibit age and size truncation relative to the Trinidad and Tobago population. Gulland (1983) observed that populations subject to heavy exploitation for long periods of time may show altered growth characteristics. McGovern et al. (1998) documented changes in the sex ratio and size at maturity of Gags *Mycteroperca microlepis* after two decades of heavy fishing pressure. Although Yellowmouth Grouper in the SEUS have been exploited for more than three decades, it is difficult to discern this rate of exploitation because Yellowmouth Grouper are less common than Scamps and Gags. Possible differences in aging techniques between our study and the Manickchand-Heileman and Phillip (2000) study could also account for some of the observed differences in longevity and growth between populations.

The value of  $M$  for wild fish populations is difficult to measure but is an important input variable for stock assessments. A single estimate of  $M$  for the entire life span of a fish, such as the estimate obtained with the Hewitt and Hoenig (2005) method, does not seem reasonable because fish become less vulnerable to large-scale predation as they attain larger sizes. Because the maximum age of Yellowmouth Grouper in this study was similar to that found by Bullock and Murphy (1994) and to the maximum ages of the species' congeners (the Gag and the Scamp), we feel that the  $M$  derived from this maximum age is a reasonable estimate for the fully recruited ages in our study, whereas it is insufficient for use with all ages. The age-varying  $M$  calculated by using the method of Charnov et al. (2013) seems to be more appropriate for the younger ages. The initial Charnov et al. (2013) estimates of  $M$ , starting with the fully recruited age of 5, are approximately double the estimate obtained from the Hewitt and Hoenig (2005) method, reflecting higher natural mortality at younger ages. The age-specific estimates of  $M$  for the older ages then stabilize near the Hewitt and Hoenig (2005)-based estimate of  $M$  (Table 2). When considering the cumulative estimate of survivorship to the oldest age, the Hewitt and Hoenig (2005) method estimates 2.5% survivorship, whereas the Charnov et al. (2013) method estimates 1% sur-

ivorship. Very few fish in our samples (19 of 388 fish) were older than 17 years, and only 1% of our fish were 22 years or older. Although sample sizes for this study were limited, the age frequency suggests that survivorship to the oldest age may truly be as low as 1%. There is no evidence that hook-and-line gear is dome selective for the Yellowmouth Grouper or its congeners; thus, the capture methods in our study had the potential to collect the largest and oldest fish in the population. These observations give weight to the argument that the Charnov et al. (2013)-based estimates of  $M$  at age should be used.

The estimates of  $M$  are most influenced by the value of  $K$ . We calculated the sensitivity of  $M$  to changes in each parameter ( $L_\infty$ ,  $K$ ) while holding the other parameter constant. As expected, changes of  $\pm 10\%$  in  $K$  resulted in average changes of 6.5% in  $M$  across all age-classes, while varying  $L_\infty$  had no effect on the estimate of  $M$  (average change =  $7.41 \times 10^{-15}$ , or functionally zero). The age-specific estimate of  $M$  from the Charnov et al. (2013) equation uses only  $L_\infty$  and  $K$  from the von Bertalanffy growth model and essentially assumes that  $t_0$  is equal to 0. When the von Bertalanffy parameters were re-estimated using the size limit correction and the constraint  $t_0 = 0$ , the value of  $K$  increased measurably due to the steepness of the initial part of the growth curve. The starting value of  $M$  at age 0.5 years was almost six times higher than that obtained when using the  $L_\infty$  and  $K$ -values from the size-limit-corrected growth model with an unconstrained  $t_0$  and was 17 times higher than that obtained when using the parameter values from the uncorrected growth model. The values of  $M$  started to converge by age 7. Although the estimated  $L_\infty$  was lowest for the size-limit-corrected model with the constrained  $t_0$ , the values of  $M$  remained the highest at all ages and were also higher than the Hewitt and Hoenig (2005) point estimate. These higher estimates of  $M$  may have a measurable impact on stock assessment models; thus, we recommend that sensitivity analyses be conducted for this range of  $M$ -values.

Although Scamps and Yellowmouth Grouper are congeners with remarkable similarity in appearance, the results of this study show that the growth model parameters for the two species are markedly different. Scamps achieve a much larger  $L_\infty$  and do so at a faster rate ( $K$ ) than Yellowmouth Grouper. These results would seem to preclude either species from being used as a proxy for the other in management scenarios. Because of the differences between the Scamp and Yellowmouth Grouper, it is imperative that proper training in identifying these species be provided to the port agents assigned to sample them from the landings of commercial and recreational vessels in the SEUS. Misidentification could lead to the biasing of growth estimates due to inclusion of otoliths from slower-growing Yellowmouth Grouper in a Scamp aging study or otoliths from faster-growing Scamps in a Yellowmouth Grouper aging study.

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