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ASPECTS OF THE LIFE HISTORY OF THE YELLOWMOUTH GROUPER, *MYCTEROPERCA INTERSTITIALIS*, IN THE EASTERN GULF OF MEXICO

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ABSTRACT

We describe the life history of yellowmouth grouper, *Mycteroperca interstitialis*, using specimens captured at the Florida Middle Ground in the eastern Gulf of Mexico between May 1978 and July 1992. Spawning occurred throughout the year; peak activity was observed during April and May. Yellowmouth grouper are protogynous hermaphrodites: sex-inversion was documented for five individuals, younger/smaller individuals were female, and most older/larger fish were male. Females began to mature at 400 mm total length (TL) or age 2; all were mature by 450 mm or age 4. Transitional fish ranged 505–643 mm and were 5 to 14 years old. The smallest and youngest mature male was 505 mm and age 4. Ages could be readily determined from otolith sections because they contained distinct opaque bands that formed during the late summer and fall. Females ranged 2 to 17 years old; males were 4 to 28 years of age. Annual growth of yellowmouth grouper averaged greater than 200 mm or 470 g during their first 2 years of life and then slowed thereafter to about 18 mm or 221 g for females and to about 10 mm or 190 g for males. Significantly different linear growth models fit sex-specific length-at-age and weight-at-age data well. Length-age and weight-age relations for all fish were: $l_t = 828\ (1 - \exp(-0.076(t + 7.5)))$ and $w_t = 13.9\ (1 - \exp(-0.022(t + 1.4)))$, where l_t is TL in mm, w_t is weight in kg, and t is age in years. The pooled estimate of total annual mortality for ages 8–18 during 1978–1992 was about 25%. Because of similarities in their morphology and habitat preference, we compared our findings for yellowmouth grouper with life-history aspects of its closely related congener, the scamp (*M. phenax*).

The yellowmouth grouper, *Mycteroperca interstitialis,* occurs off Bermuda and the Bahama Islands, from North Carolina southward to the Florida Keys, throughout the Gulf of Mexico and Caribbean Sea, and southward to Brazil (Smith, 1971). This species occurs at depths greater than about 30 m in the eastern Gulf of Mexico, but it may be found at shallower depths in Bermuda and the Florida Keys (Bardach et al., 1958; Bullock and Smith, 1991).

Mycteroperca interstitialis bears a striking resemblance to its closely related congener, the scamp (*M. phenax*), in body proportions, color pattern (Bullock and Smith, 1991; p. 235, pl. XV C, D; p. 239, pl. XVII A, B) and meristic characters (Smith, 1971). Because yellowmouth grouper was often misidentified as scamp, it was not documented until the mid-1970s that *M. interstitialis* was sympatric with *M. phenax* at the Florida Middle Ground (a reef biotope located on the outer west Florida shelf at 28°15′–45′N, 84°00′–25′W) (Smith et al., 1975). Because of the two species' similarity, scamp and yellowmouth grouper are marketed locally under one name—scamp. The yellowmouth grouper's contribution to "scamp" landings is low; however, the exact proportion is unknown.

To properly manage the multi-species grouper fishery, it is important to recognize the coexistence of two closely related species and to understand differences in their life histories. Variation in life-history strategies may cause each species to respond differently to fishing pressure (Adams, 1980).

Little information is available on the life history and population dynamics of *M. interstitialis,* despite its commercial importance in Bermuda and other areas such as Venezuela (Smith, 1971). Bardach et al. (1958) described its juvenile color phases, time of spawning, and depth range and estimated the duration of its larval stage off Bermuda. Food habits of yellowmouth grouper from the Bahamas were documented by Randall (1967). Thompson and Munro (1978) noted that individuals had ripe gonads during April in Jamaican waters. Bullock and Smith (1991) described the spawning period, fecundity, dietary items, length-weight relationship, and parasites associated with yellowmouth grouper from the eastern Gulf of Mexico.

In this paper we describe aspects of the basic life history of yellowmouth grouper inhabiting the Florida Middle Ground. We provide information on size and age at maturity, age and growth, and total annual mortality. We also update previous findings on protogynous hermaphroditism, spawning periodicity, length-weight relationship, and dietary habits (Bullock and Smith, 1991). This information is compared with the life history and population dynamics of scamp in the eastern Gulf of Mexico and the U.S. South Atlantic region. Finally, we describe a gonad condition in *M. interstitialis* and other groupers that may lead to the loss of reproductive potential.

METHODS AND MATERIALS

All specimens (N = 224), which were caught by anglers fishing the Florida Middle Ground aboard partyboats, were sampled dockside at Johns Pass, Pinellas County, Florida. Aperiodic sampling was carried out from May 1978 through July 1992. Whole specimens were weighed to the nearest ounce (W, converted to kilograms) and measured to the nearest millimeter for standard length (SL), fork length (FL), and total length (TL). All lengths are reported as total length unless otherwise noted. Gonads were excised and preserved in 10% formalin. Otoliths (sagittae) were removed and stored dry in vials. The same sampling techniques were used for scamp except that scamp were captured throughout the eastern Gulf of Mexico (Hood et al., 1990).

In the laboratory, gonads were washed in water and stored in 70% ethanol. Gonadal material was embedded in paraffin or plastic (glycol methacrylate), sectioned to a thickness of 3.5 μm, and stained with Weigert's haematoxylin and eosin Y. Processed sections were examined under a compound microscope and were assigned to gonad-development classes adapted from Moe's (1969) criteria for red grouper, *Epinephelus morio*. Briefly, these classes are listed as follows for females: immature, mature resting, mature active or ripe (individuals with vitellogenic oocytes), and spent. Male development classes are as follows: immature, mature inactive, ripening mature, ripe, and postspawning.

Diameters of the 10 largest developing oocytes measured from each histological section were used to determine the time of peak spawning. These measurements were recorded using OPTIMAS, an electronic image processing software package that employs a video camera mounted on a compound microscope. We did not measure degenerating vitellogenic oocytes because they would erroneously elevate the mean oocyte size.

Although adult yellowmouth grouper and scamp are very similar in appearance, the two species can be distinguished by color pattern (the yellowmouth grouper lacks well-separated spots found on scamp) and by the shape of the caudal fin (Smith, 1971). In both species, specific caudal fin rays elongate as body size increases (pers. observ.), giving the caudal fins their distinctive shapes (Fig. 1). We used measurements of these elongated caudal rays to determine if caudal fin shape was sexually dimorphic in each species. Analysis of covariance (ANCOVA) was used to compare the lengths of the medial caudal fin exsertions of male and female yellowmouth grouper and to compare the dorsal lobe lengths of the caudal fins (i.e., total length minus fork length) of male and female scamp captured in the eastern Gulf of Mexico (N = 695; Bullock and Smith, 1991).

A Buehler Isomet low-speed saw was used to cut four 0.5-mm transverse sections from each otolith. Sections were cut as close to the core as possible. The sections were mounted on microscope slides using Histomount mounting medium and were viewed through a dissecting microscope using reflected light. Opaque bands were enumerated independently by two readers and the counts were compared. In cases where counts differed by one or two, a joint reading was made to determine a final count. Otoliths for which counts made by the independent readers differed by more than two were deleted from the analysis.

We used a generalized model (Schnute, 1981) in deciding on appropriate equations for modelling yellowmouth grouper growth. This generalized model allowed us to compare a 4-parameter growth model to models with fewer parameters so that we could test whether significant increases in unexplained variation occurred as parameters were deleted. Differences in unexplained variation between models were evaluated using a variance-ratio test. We compared growth models of males and females

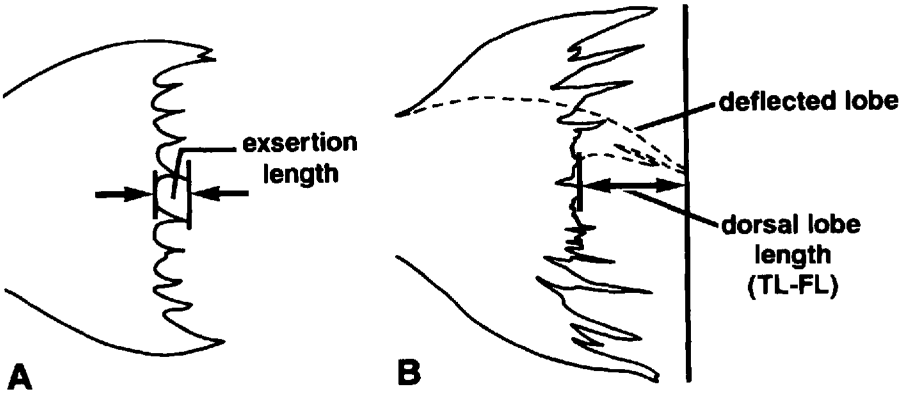

Figure 1. Caudal fin profiles of adult (A) *Mycteroperca interstitialis* and (B) *M. phenax* and depiction of method of measurement.

by using ANCOVA for linear models (Snedecor and Cochran, 1967) and likelihood-ratio tests for nonlinear models (Kimura, 1980; Cerrato, 1990). Weight-length relationships were calculated using the allometric model $W = a\mathrm{TL}^b$, fit using nonlinear regression techniques (SAS Institute, Inc., 1982), and compared using likelihood-ratio tests. Length-length relationships were calculated using a generalized linear model (SAS Institute, Inc., 1982).

Least-square regression of catch curve data (Jensen, 1985) was used to estimate instantaneous mortality (Z). The point at which full recruitment occurred for yellowmouth grouper was not clear from our data. Therefore, we used a Student *t*-test to compare an estimate of mortality from data that included fish one or more years older than the most likely age of recruitment to an estimate of mortality made from data that included fish one year younger than the most likely age at recruitment. Catch curve data were truncated at an age for which fewer than three fish occurred in any older age group (Chapman and Robson, 1960).

RESULTS

Reproduction.—Yellowmouth grouper seemingly spawn throughout the year; peak activity occurs during April and May. Ripe females, those with vitellogenic oocytes, occurred throughout the year, but mean oocyte diameters were at a maximum and all observed ovaries were ripe during April or May (Figs. 2, 3). Spent females were sampled during August (N = 4), September (N = 2), and December (N = 1), indicating a refractory period during the late summer or fall. Also, during this time period mean oocyte diameters were at a minimum, and the highest number of mature resting females were sampled. Male reproductive activity paralleled that of females. Ripe or ripening mature males occurred throughout the year. Most ripe males were found during May. Spent males were captured during May, July–October, and December (Fig. 2).

Examination of histologically prepared tissues from five individuals revealed evidence for protogyny in yellowmouth grouper (Fig. 4). Proliferating sperm cysts were noted among degenerating oocytes. Individual transitional fish were captured in February 1982, March 1991, May 1978, July 1981, and August 1987 (Fig. 2).

Sex ratios changed as size and age increased, further evidence of protogynous hermaphroditism. All fish less than 500 mm and younger than age 4 were female; all fish larger than 749 mm and older than 17 years were male. The proportion of males within 50-mm size classes of 500–549, 550–599, 600–649, 650–699, and 700–749 mm was 0.15, 0.38, 0.50, 0.75, and 0.69, respectively. Twenty-two percent of the fish less than 10 years old were males, whereas 64% and 88% of

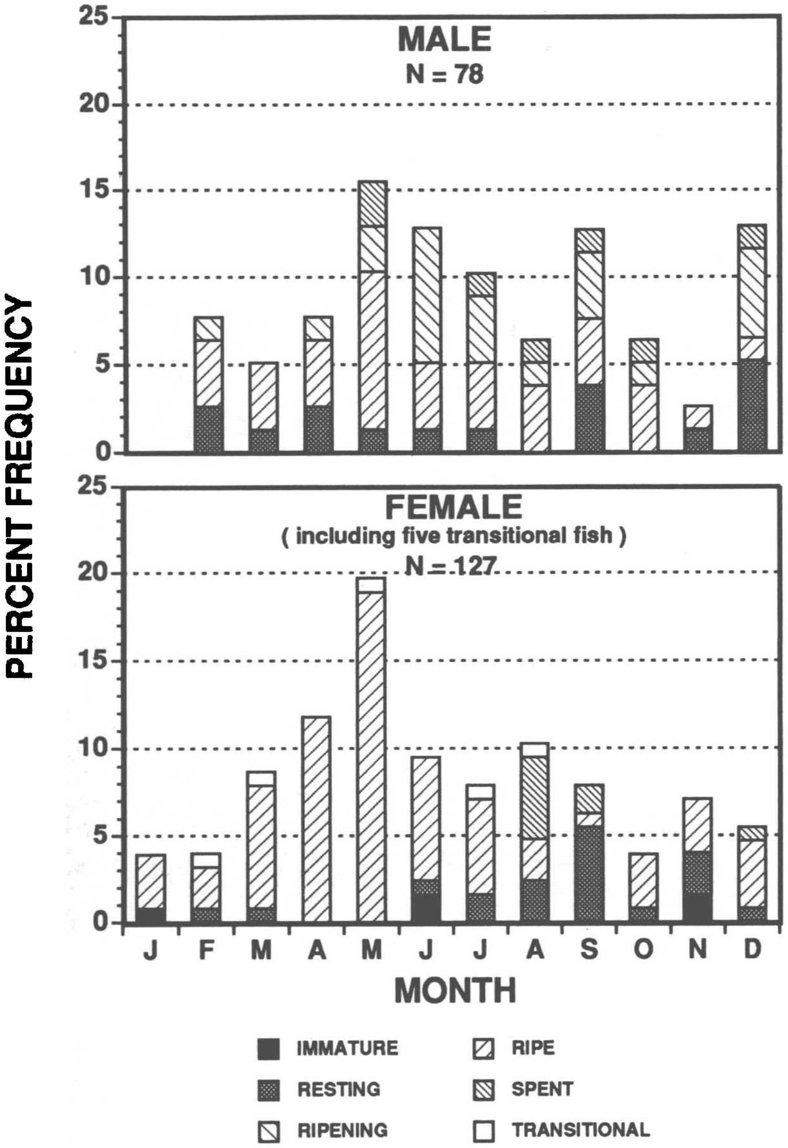

Figure 2. Monthly percent frequencies of gonad classes for male and female *Mycteroperca interstitialis* sampled from catches made at the Florida Middle Ground between May 1978 and July 1992.

the fish greater than or equal to 10 or 15 years old, respectively, were males. Two females, 16 and 17 years old, were markedly older than most of the other females sampled (the next oldest female was 13 years old) possibly indicating that some females do not change sex.

Yellowmouth grouper mature as females between 400 mm and 450 mm and between 2 and 4 years of age. The smallest and youngest mature females were 420 mm and 2 years old (Tables 1, 2). All females 450 mm or larger and 4 years old or older were mature. Transitional fish were 503–643 mm in length

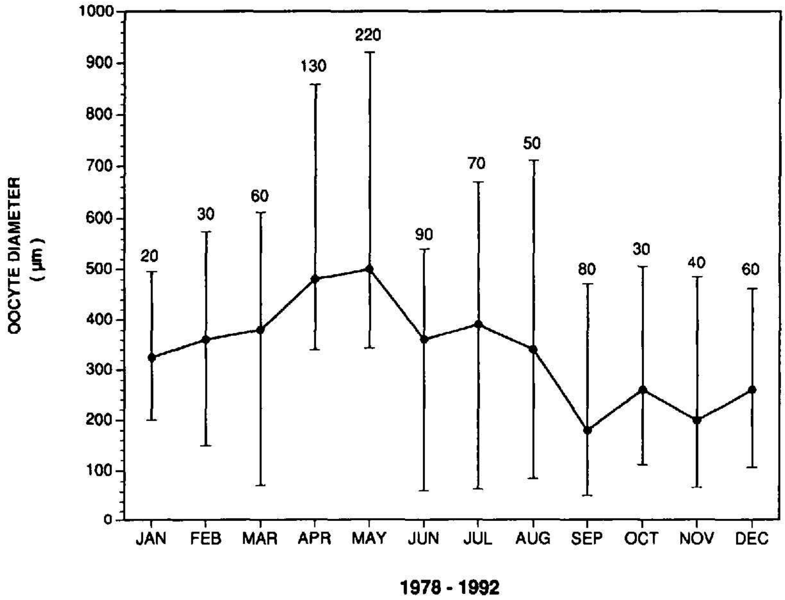

Figure 3. Monthly mean diameters of the ten largest oocytes per histological section for *Mycteroperca interstitialis* sampled from catches made on the Florida Middle Ground between May 1978 and July 1992. Minimum and maximum values and number of oocytes measured are given.

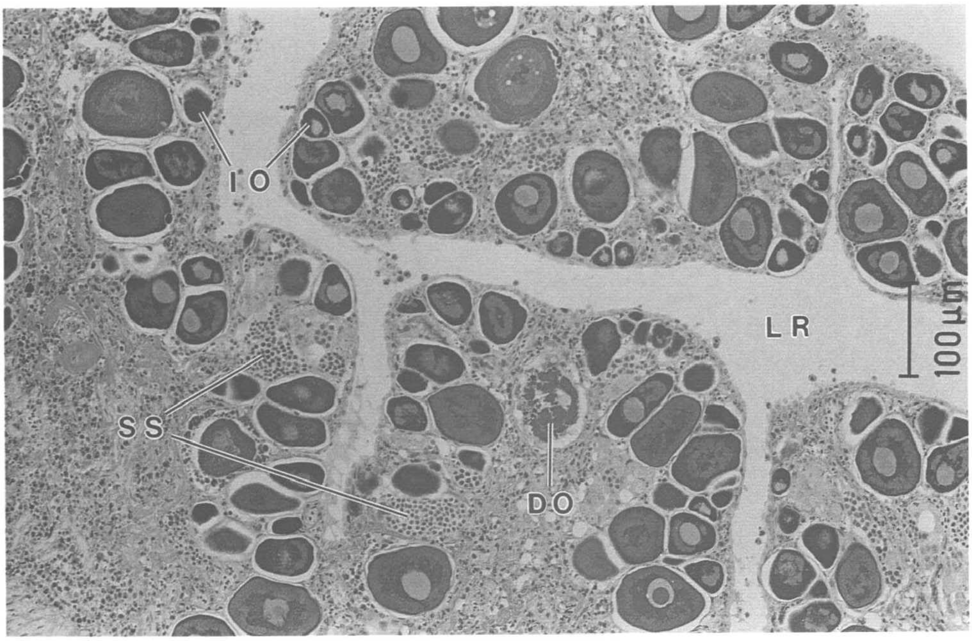

Figure 4. Photomicrograph of proliferating male tissue in a transitional gonad from *Mycteroperca interstitialis* (503 mm; age 5) captured at the Florida Middle Ground during March 1991. DO = degenerating oocyte; IO = immature oocyte; LR = lumen remnant; SS = secondary spermatocytes; scale bar = 100 µm.

Table 1. Percentage of mature female and male *Mycteroperca interstitialis* by 50-mm size classes. Mature fish are defined as those with gonads in mature resting, mature active, or spent classes for females or in mature inactive, ripening mature, ripe or postspawning classes for males (sensu Moe, 1969).

Size class (mm TL)	Females			Males		
	N	Mature	% Mature	N	Mature	% Mature
350–399	2	0	0	0	0	—
400–449	6	4	67	0	0	—
450–499	21	21	100	0	0	—
500–549	34	34	100	6	6	100
550–599	29	29	100	18	18	100
600–649	18	18	100	18	18	100
650–699	7	7	100	21	21	100
700–749	4	4	100	9	9	100
750–799	0	—	—	6	6	100

and 5–14 years of age. All males in our samples were mature. Males first appeared in the population at about 500–549 mm and 4 years of age (Tables 1, 2). The smallest and youngest males were 505 mm and 4 years of age.

The relative length of the medial caudal fin exsertion within each sex was highly variable and not sexually dimorphic. There was a significant positive relation between exsertion length and standard length for both males and females, but the variables were not highly correlated (females, $r^2 = 0.12$; males, $r^2 = 0.24$). There was no significant difference in slopes between sexes (ANCOVA, $F = 1.12$, 1, 132 df, $P = 0.29$), but elevations were significantly different ($F = 4.29$, 1, 133 df, $P = 0.04$). We attribute the difference in elevation to the observed differences in the distributions of the sizes of males and females. Most smaller fish were female and most larger fish were male. Therefore, while elevations or "adjusted means" were different, very little actual difference was observed in the relative length of the caudal fin exsertion between sexes.

Table 2. Percentage of mature female and male *Mycteroperca interstitialis* by age group

Age (years)	Females			Males		
	N	Mature	% Mature	N	Mature	% Mature
2	3	1	33	0	—	—
3	4	2	50	0	—	—
4	7	7	100	1	1	100
5	12	12	100	2	2	100
6	13	13	100	4	4	100
7	24	24	100	4	4	100
8	14	14	100	5	5	100
9	9	9	100	8	8	100
10	11	11	100	12	12	100
11	5	5	100	7	7	100
12	3	3	100	6	6	100
13	4	4	100	3	3	100
14	0	—	—	3	3	100
15	0	—	—	1	1	100
16	1	1	100	2	2	100
17	1	1	100	3	3	100
18	0	—	—	3	3	100
19	0	—	—	1	1	100
≥20	0	—	—	5	5	100

Figure 5. A hardened mass of degenerated ovarian tissue found in a reproductively active male *Mycteroperca interstitialis* (598 mm; age 9).

We also noted a gonad abnormality that has rarely been described in the literature on groupers. The testis of a reproductively active, 9-year-old male (598 mm, 2.7 kg) captured in April 1991 contained a hardened mass that seemed to be composed of partially degenerated ovarian tissue (Fig. 5). This individual had undergone sex inversion but had retained unshed eggs in the lumen of the testis. The hardened mass occupied a major portion of both lobes of the testis.

Age and Growth.—Ages could be determined for 203 of the 213 fish examined. Sections from four otoliths were deemed illegible. The otolith counts made by the independent readers agreed for 104 otolith sections (49%). In the majority

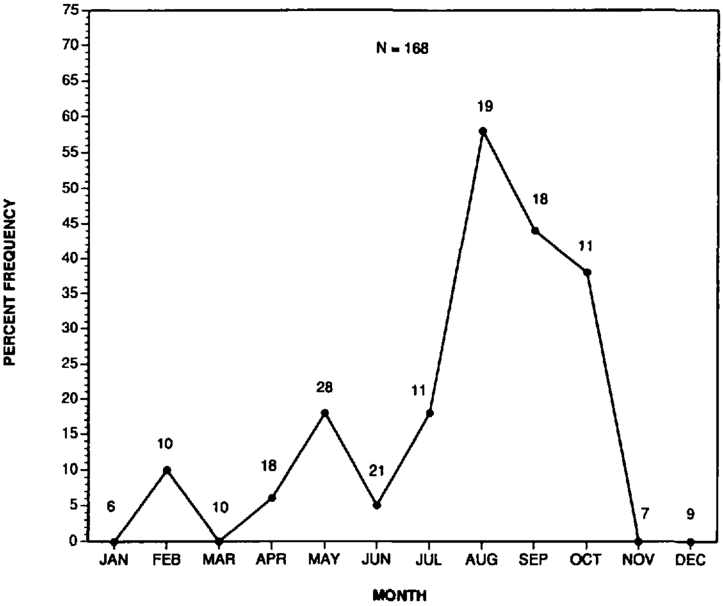

Figure 6. Monthly percentage of *Mycteroperca interstitialis* with otoliths lacking a marginal increment.

of cases in which the counts of opaque bands (99/105 sections) differed, they differed only by one (N = 66) or two (N = 33). Differences in counts were resolved for all of these otoliths during a joint reading. Counts from six otolith sections differed by three or four. These otoliths, along with the four otoliths originally determined to be illegible, were discarded from the analysis of growth and mortality.

Opaque bands were deposited during the late summer and early fall for most yellowmouth grouper, evidently once each year. Over 80% of fish sampled during the months of November through July had deposited additional translucent matrix since the formation of the most recent opaque band (Fig. 6). In August–October, 40–60% of fish had opaque bands at the margin of their otoliths. An opaque band was found at the margin of the otolith sections of single fish collected in February, April, and June and of five specimens collected in May. This suggests that either the period of opaque band formation is protracted, that formation occurs at different times among age classes, or that some fish may form more than one opaque band each year. However, for this report we assume that all sampled fish had formed one opaque band per year.

Ages of females ranged from 2 to 17 years; males were 4 to 28 years old. Individuals undergoing sex inversion were 5, 6, 10 (two specimens), or 14 years old.

Yellowmouth grouper grow rapidly in length and weight during their first 2 years, after which growth slows markedly. The average observed length of age-2 females, the youngest fish collected, was 415 mm, implying a growth rate of more than 200 mm per year between ages 0 and 2 (Table 3). This contrasts with the slower growth observed between ages 2 and 5, when average observed lengths of females increased from 415 to 492 mm, a rate of approximately 25 mm per year. A similar reduction in weight gain was observed, decreasing from 500 g

Table 3. Average observed and predicted total lengths (mm) at age for female and male *Mycteroperca interstitialis*. Predicted lengths are those calculated from the sex-specific linear growth models fit to length and age data (see text).

	Female			Male		
Age (years)	N	Average observed	Predicted	N	Average observed	Predicted
2	3	415	447			
3	4	439	465			
4	7	498	484	1	561	561
5	12	492	503	2	534	571
6	13	547	522	4	581	581
7	24	545	541	4	572	591
8	14	559	560	5	607	602
9	9	579	578	8	610	612
10	11	593	597	12	619	622
11	5	566	616	7	654	632
12	3	642	635	6	636	642
13	4	674	654	3	637	653
14	0	—	672	3	699	663
15	0	—	691	1	690	673
16	1	747	710	2	727	683
17	1	694	729	3	686	694
18				3	698	704
19				1	730	714
20				0	—	724
21				2	725	734
22				0	—	745
23				0	—	755
24				1	793	765
25				0	—	775
26				0	—	785
27				0	—	796
28				2	761	806

per year between ages 0 and 2 to about 200 g per year between ages 2 and 5 (Table 4).

Growth in length was more rapid for females than for males; growth in weight did not differ between sexes. Growth rates averaged 18.8 mm or 221 g per year for females 2–17 years old. Growth averaged 10.2 mm or 190 g per year for males 4–28 years old. Growth rates were significantly different between sexes in terms of length (ANCOVA, $F = 22.86$, 1, 177 df, $P < 0.0001$) but not in terms of weight (ANCOVA, $F = 1.03$, 1, 153 df, $P = 0.31$).

Linear growth models fit the data well over the age range sampled for each sex (Tables 3, 4). Variance-ratio tests showed no significant differences between the fit of the data to linear models of growth and the fit to the 4-parameter generalized models (in terms of length: females, $F = 1.53$, 2, 109 df, $P = 0.22$; males, $F = 2.09$, 2, 68 df, $P = 0.13$). Linear growth models (with standard errors of parameters in parentheses) for each sex (Figs. 7, 8) are as follows:

FEMALES:

$$l_t = \underset{(12.27)}{408.9} + \underset{(1.535)}{18.83(t)} \qquad N = 111, \quad r^2 = 0.580$$

$$w_t = \underset{(0.1866)}{0.623} + \underset{(0.0241)}{0.221(t)} \qquad N = 95, \quad r^2 = 0.473$$

Table 4. Average observed and predicted weight (kg) at age for female and male *Mycteroperca interstitialis*. Predicted weights are those calculated from the sex-specific linear growth models fit to weight and age data (see text).

	Female			Male		
Age (years)	N	Average observed	Predicted	N	Average observed	Predicted
2	3	1.0	1.1			
3	3	1.2	1.3			
4	6	1.8	1.5	1	2.2	2.1
5	11	1.6	1.7	2	2.2	2.3
6	13	2.2	1.9	4	2.5	2.5
7	21	2.2	2.2	4	2.6	2.7
8	11	2.2	2.4	4	3.0	2.9
9	9	2.5	2.6	7	2.8	3.0
10	8	2.7	2.8	12	3.2	3.2
11	4	2.4	3.1	7	3.7	3.4
12	2	3.3	3.3	4	3.6	3.6
13	3	3.9	3.5	3	3.1	3.8
14	0	—	3.7	3	4.5	4.0
15	0	—	3.9	1	4.1	4.2
16	1	5.7	4.2	2	4.9	4.4
17	0	—	4.4	2	4.8	4.6
18				2	4.6	4.7
19				1	4.8	4.9
20				0	—	5.1
21				1	5.5	5.3
22				0	—	5.5
23				0	—	5.7
24				1	6.2	5.9
25				0	—	6.1
26				0	—	6.3
27				0	—	6.5
28				1	5.8	6.6

MALES:

$$l_t = \underset{(12.28)}{520.0} + \underset{(0.965)}{10.21}(t) \qquad N = 70, \quad r^2 = 0.622$$

$$w_t = \underset{(0.2219)}{1.331} + \underset{(0.0183)}{0.190}(t) \qquad N = 62, \quad r^2 = 0.641,$$

where l_t is TL in mm, w_t is weight in kg, and t is age in years. Whereas there was no significant difference between the growth rates of females and males, in terms of weight, a significant difference between the elevations of the regressions of weight on age (ANCOVA, $F = 14.22$, 1, 154 df, $P = 0.0002$) justified the use of separate linear growth models for each sex.

The combined data for sizes and ages of females, transitionals, and males showed some indication of curvature and fit the following von Bertalanffy growth models (Figs. 7, 8):

$$l_t = \underset{(45.0)}{828}(1 - \exp(-\underset{(0.0158)}{0.076}(t + \underset{(1.61)}{7.5}))) \qquad N = 200, \quad r^2 = 0.726$$

$$w_t = \underset{(7.86)}{13.9}(1 - \exp(-\underset{(0.0163)}{0.022}(t + \underset{(1.15)}{1.4}))) \qquad N = 165, \quad r^2 = 0.642$$

Length and weight data indicated that the youngest males may have been derived from the largest females in their age group. Although age-4 females ranged

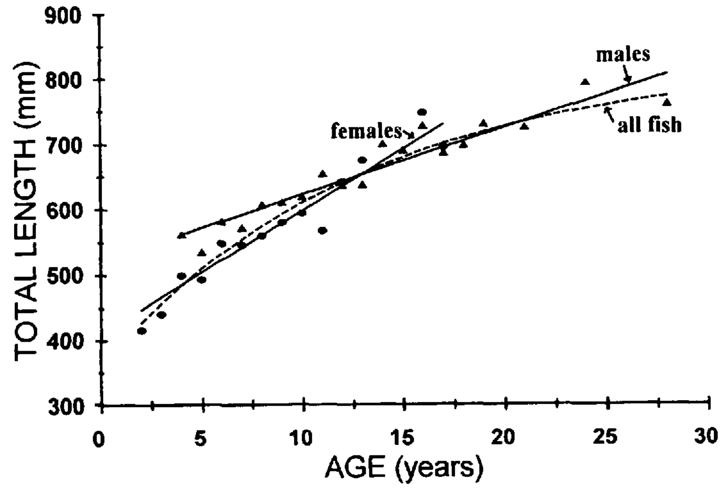

Figure 7. Average observed length (mm) at age for female (●) and male (▲) *Mycteroperca interstitialis* sampled from the Florida Middle Ground between May 1978 and July 1992. Lines represent predicted lengths from sex-specific linear growth models: mm TL = 409 + 18.8(AGE, yr) for females; mm TL = 520 + 10.2(AGE, yr) for males; and from a von Bertalanffy growth model for all fish (– – –): mm TL = 828 (1 − exp(−0.076(AGE + 7.5))).

445–564 mm (1191–2523 g), the only age-4 male in our sample was 561 mm (2155 g). At age 5, females ranged 458–525 mm (1134–2495 g), whereas males were 523 mm (1928 g) and 544 mm (2381 g). Sizes of older males and females overlapped more, although through age 11 the smallest fish of any given age was a female (Fig. 7). Transitional individuals were about the same size as or smaller

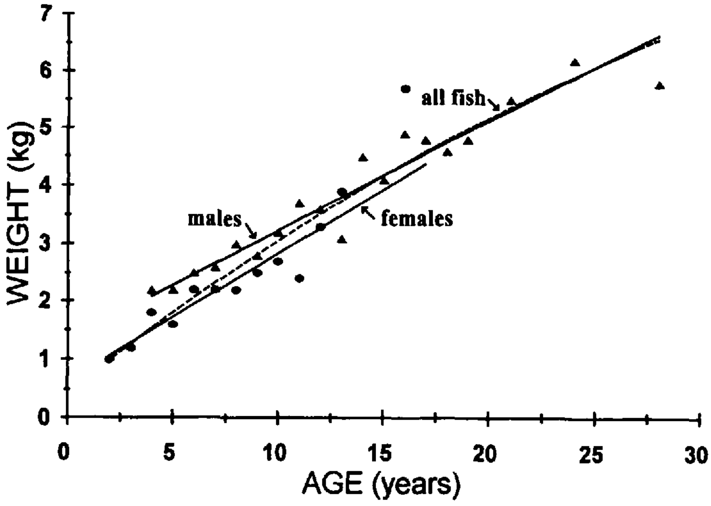

Figure 8. Average observed weight (kg) at age for female (●) and male (▲) *Mycteroperca interstitialis* sampled from the Florida Middle Ground between May 1978 and July 1992. Lines represent predicted lengths from sex-specific linear growth models: W (kg) = 0.62 + 0.22(AGE, yr) for females; W (kg) = 1.33 + 0.19(AGE, yr) for males; and from a von Bertalanffy growth model for all fish (– – –): W (kg) = 13.9 (1 − exp(−0.022(AGE + 1.4))).

Table 5. Length–weight and length–length relations for *Mycteroperca interstitialis*. Ranges indicated are for the independent variable in the regression equation.

Equation	N	Length range	r^2
$TL = 14.722 + 1.2054(SL)$	223	91–646	0.995
$SL = -9.695 + 0.8253(TL)$	223	116–793	0.995
$FL = 11.175 + 1.1721(SL)$	182	91–631	0.995
$SL = -7.253 + 0.8491(FL)$	182	115–749	0.995
$FL = 0.225 + 0.9658(TL)$	183	116–780	0.998
$TL = 1.008 + 1.0331(FL)$	183	115–749	0.998
$W = 0.000025855 * TL^{2.89367}$	178	367–793	

than the average-sized females at ages 5 and 6, and they were larger than the average-sized females at ages 10 and 14.

Weight-length relationships were similar for males and females. Likelihood-ratio tests indicated no significant differences between male and female estimates for "b" ($\chi^2 = 0.25$, 1 df, $P = 0.62$) or "a" ($\chi^2 = 0.22$, 1 df, $P = 0.64$) in the allometric model $W = a\mathrm{TL}^b$. Yellowmouth grouper averaged 0.9 kg at 400 mm, 2.8 kg at 600 mm, and 6.5 kg at 800 mm. Weight-length and length-length relationships and associated statistics are given in Table 5.

Diet.—Prey items occurred in 25 of 188 stomachs examined (Table 6). The diet was made up entirely of fishes; *Chromis* spp. comprised 40% by frequency of occurrence and 38% by number of prey. Other prey items were typical reef-dwelling fishes in the families Apogonidae, Carangidae, Haemulidae, Gobiidae, Lutjanidae, Scaridae, and Synodontidae.

Mortality.—A pooled estimate of total annual mortality ($1 - e^{-z}$) and 95% confidence limits for the 1978–1992 sampling period was 0.25 ± 0.13 for fish 8–18 years old. Estimates of instantaneous total mortality rate (standard error) were 0.28 (0.083) for fish 10–18 years old and 0.25 (0.055) for fish 8–18 years old. These estimates were not significantly different (ANCOVA; slopes, $F = 0.09$, 1, 16 df, $P = 0.79$); therefore, recruitment seemed to be complete by age 8.

Table 6. Percent frequency of occurrence and percent number of prey items found in *Mycteroperca interstitialis* stomachs. Prey items occurred in 25 of 188 stomachs examined.

Prey item	Occurrence	
	Percent frequency	Percent number
Chromis enchrysurus	4.0	2.9
Chromis insolatus	4.0	2.9
Chromis scotti	8.0	5.9
Chromis spp.	24.0	26.5
Apogonidae	4.0	2.9
Decapterus punctatus	4.0	2.9
Haemulidae	4.0	2.9
Haemulon aurolineatum	4.0	11.8
Ioglossus calliurus	8.0	8.8
Rhomboplites aurorubens	8.0	8.8
Scarus sp.	4.0	2.9
Synodontidae	8.0	5.9
Synodus intermediatus	4.0	2.9
Osteichthyes	12.0	11.8

DISCUSSION

Reproduction.—Peak spawning in yellowmouth grouper and scamp roughly coincide. However, female yellowmouth grouper are ripe over a more protracted period than female scamp are. Scamp spawning occurs from December through July; peak activity takes place in May and June (Hood et al., 1990). We found that yellowmouth grouper spawning occurs throughout the year and that peak activity occurs in April and May. Differences in the time frames during which scamp and yellowmouth grouper were sampled may explain some of the differences observed in spawning periodicity. The time frame for sampling scamp was relatively discrete (November 1977 to June 1980) compared to the period during which we sampled yellowmouth grouper (May 1978 to July 1992). The latter, long-term sampling program offered a greater opportunity to sample fish during unusually early or late spawning seasons.

Because spawning occurs throughout the year, it is unlikely that yellowmouth grouper form massive spawning aggregations containing hundreds to thousands of individuals as has been reported for Nassau grouper, *Epinephelus striatus* (Smith, 1972). Yellowmouth grouper aggregations may occur during peak spawning in April and May, and smaller-group matings may occur throughout the balance of the year. Scamp aggregations of approximately 100 individuals, exhibiting possible spawning behavior and coloration, have been observed off the east coast of Florida during September 1978, September 1979, and April 1980 in about 80 m of water (Gilmore and Jones, 1992).

Female yellowmouth grouper reach sexual maturity at the same age but at slightly larger sizes than do scamp in the eastern Gulf of Mexico. The youngest mature female yellowmouth grouper was 2 years old, and all females were mature by age 4. In the eastern Gulf of Mexico, scamp become sexually mature between age 2 and age 5 (Hood et al., 1990). Female yellowmouth grouper attain sexual maturity at 387–435 mm FL (400–450 mm TL), whereas female scamp are mature at 275–400 mm FL (Hood et al., 1990).

The medial caudal fin exsertion in yellowmouth grouper is not a sexually dimorphic character. In fact, obvious sexual dimorphism is not apparent in many species of groupers, although male gag (*M. microlepis*) seem to acquire dark pigmentation on the belly, at least at large sizes (Bullock and Smith, 1991; Gilmore and Jones, 1992). Gilmore and Jones (1992) observed ten male scamp with long caudal fin exsertions, which suggests sexual dimorphism in scamp. However, we found no correlation between caudal fin dorsal lobe length and sex in scamp from the eastern Gulf of Mexico (unpubl. data).

The presence of transitional individuals in our sample confirms that yellowmouth grouper are protogynous hermaphrodites. Smith (1959) concluded that the yellowmouth grouper was a protogynous hermaphrodite based on histological data from nine females. However, Shapiro (1987) did not include this species with other serranids for which he felt that reasonable evidence of protogyny had been found. Bullock and Smith (1991) subsequently found what they considered to be a transitional individual. In the present study, four additional transitional individuals were identified.

Our data indicate that yellowmouth grouper are functional females prior to sex inversion. In some fishes, previtellogenic and advanced oocytes may be present in an immature ovariform (=nonfunctional) gonad (sensu Cole and Shapiro, 1992), and males can be derived directly from these nonfunctional female-like individuals. However, in fishes that show this type of reproductive strategy, immature individuals (i.e., those with a nonfunctional ovariform gonad) that are as large as the smallest males should occur in the population. This was not the case for yellowmouth grouper. All immature female yellowmouth grouper in our samples were at least 50 mm smaller than the smallest male. We believe that this supports our contention that all yellowmouth grouper initially function as females.

The occurrence of hardened ovarian masses in groupers, although not widely documented, has been observed in several species collected from the eastern Gulf of Mexico. This condition, which would undoubtedly lead to reduced reproductive potential, has been observed in scamp and yellowedge grouper, *Epinephelus flavolimbatus* (Bullock and Smith, 1991); and in jewfish, *E. itajara,* and in the graysby, *E. cruentatus* (pers. observ.). We speculate that the retention of unviable eggs during the spawning season may be caused by physical trauma, termination of male behavioral cues just prior to spawning, or lack of an adequate number of males needed to initiate egg release from all females, especially in group spawners.

Age and Growth.—The growth of yellowmouth grouper described here is essentially that of mature females and males. Our samples contained very few immature females; all males were mature. The slow, nearly linear growth of mature fish cannot be extrapolated to young, immature fish (i.e., to ages 0–1). These fish must grow more rapidly than older ones. Slower growth after age 2 may reflect the greater physiological and behavioral investment in reproduction that occurs in mature individuals.

In the eastern Gulf of Mexico, yellowmouth grouper are, on average, larger than scamp of the same age. Scamp grow more rapidly in a relative sense ($K = 0.15 \cdot yr^{-1}$, Hood et al., 1990; $K = 0.08 \cdot yr^{-1}$ for yellowmouth grouper) but reach a smaller asymptotic length (706 mm [638 mm FL], Hood et al., 1990; 828 mm for yellowmouth grouper). Off North Carolina and South Carolina, scamp grow to a larger asymptotic length (1,105 mm [985 mm FL]) (Matheson et al., 1986) than do yellowmouth grouper in the eastern Gulf of Mexico. Yellowmouth grouper in the eastern Gulf are larger than South Atlantic scamp through age 4 but scamp continue to grow rapidly thereafter and exceed the average lengths of yellowmouth grouper by 100 mm at age 8 and by 200 mm at age 15.

Yellowmouth grouper were heavier at a given length than scamp were. Predicted weights of yellowmouth grouper measuring 200, 400, and 600 mm were 109, 850, 2827 g, respectively, whereas scamp weights were 95, 706, and 2284 g, respectively, for the same size sequence (Hood et al., 1990).

Diet.—Yellowmouth grouper are mainly piscivorous, both as juveniles and adults. In the Netherlands Antilles, Nagelkerken (1981) observed that juvenile yellowmouth grouper were never in direct contact with the corals and concluded that these juveniles fed mainly on fish. In the West Indies, Randall (1967) noted only fish in the stomach contents of yellowmouth grouper, although he examined only eight specimens. Likewise, scamp are largely piscivorous. Off North Carolina, invertebrates made up a portion of the scamp's diet; but fishes, namely unidentifiable fish remains, *Decapterus punctatus, Haemulon aurolineatum,* unidentifiable serranids, and *Rhomboplites aurorubens,* were most important (Matheson et al., 1986).

Whereas scamp are found throughout the eastern Gulf of Mexico, yellowmouth grouper tend to have a patchy distribution, which possibly reflects yellowmouth grouper's dependence upon prey such as *Chromis* spp. and its dependence upon high-relief habitat such as the Florida Middle Ground. The feeding habits of yellowmouth grouper and scamp from the eastern Gulf of Mexico appear quite similar from limited observations (Bullock and Smith, 1991). Both species, as previously noted, are principally piscivorous, and dietary overlap occurs. However, as in other serranids, dietary overlap does not seem to hinder coexistence of yellowmouth grouper and scamp at the Florida Middle Ground. Bortone et al. (1981) found little or no differences in the food habits of sympatric populations of the close congeners *Diplectrum formosum* and *D. bivittatum* near Dry Tortugas, Florida. Smale (1986) examined the feeding habits of three sparids and a grouper, *Epinephelus guaza,* off the southeastern Cape coast of South Africa and found considerable overlap in prey species. However, he concluded that overlap did not necessarily imply competition because the demand for the resources did not exceed the supply of prey species, many of which were selectively removed due to fishing pressure.

Mortality and Fishery Implications.—Our estimate of mortality is likely to be less than the present mortality rate. Our pooled estimate assumes constant recruitment and mortality (equilibrium) for each year-class considered. However, it seems likely that fishing mortality increased over the sampling period. Therefore, older fish are more abundant in our samples than would be expected under equilibrium at the present rate of mortality, resulting in a pooled estimate that is too low.

Our observed pooled mortality for yellowmouth grouper suggests that fishing mortality was at least 15% per year at the Florida Middle Ground during 1978–1992. Based on the maximum observed age of yellowmouth grouper, approximately 30 years, it is unlikely that the conditional natural mortality rate is much lower than 10% per year (an instantaneous natural mortality rate, M, of about 0.1). Given this natural mortality rate and our estimate of total mortality ($Z = 0.25$), the conditional rate of fishing mortality was slightly less than 15% per year for 8- to 18-year-old yellowmouth grouper on the Florida Middle Ground during 1978–1992. Matheson et al. (1986) estimated that total annual mortality for scamp off North Carolina and South Carolina during 1972–1979 averaged 38–47% ($Z = 0.47$–0.63) for fish 13 years of age or older. Using their estimate of M (0.21), the conditional rate of fishing mortality for scamp off the Carolinas was 23–34% per year. Our minimum estimate for yellowmouth grouper at the Florida Middle Ground is lower. However, even this level of fishing may result in a significant harvest of the available yield of yellowmouth grouper. Like other relatively large, slow-growing, long-lived species of groupers such as scamp (Matheson et al., 1986), it is possible to overfish yellowmouth grouper at low levels of exploitation. In addition, we observed that the ages of yellowmouth grouper transitionals declined during our 15-year study from 10, 10, and 14 years old between 1978 and 1982 to 5 and 6 years old between 1987 and 1991. This may be a response to exploitation. When a protogynous species experiences an increase in mortality it should theoretically preserve its sex ratio by reducing the age of transition (Charnov, 1982).

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