

Abstract.—Gag, *Mycteroperca microlepis*, is a large, slow-growing, protogynous grouper that probably makes annual migrations to specific locations to aggregate for spawning. During 1976–82, male gag constituted 19.6% of the sexually mature individuals taken during fishery-dependent and fishery-independent sampling along the southeast coast of the United States. A similar percentage of males was found in the Gulf of Mexico from 1977 to 1980; however, males made up only 1.9% of the population in the Gulf of Mexico during 1992. To assess the current sex ratio of gag along the southeast U.S. coast, an emergency rule was enacted by the Department of Commerce in January 1995 that required commercial vessels from North Carolina to southeast Florida to land gag with gonads intact. Histological examination of 2613 gonads of sexually mature gag collected from 18 January through 18 April 1995 revealed that 5.5% of the gag from the southeast Atlantic were male. There was a weak trend indicating that females reached maturity at a smaller size in 1994–95 than in 1976–82. Very few transitional specimens were collected during the spawning season. Most transitional individuals (79%) were taken during April through June immediately after the 1995 spawning season. Gag in spawning condition were landed during December through mid-May by fishermen working offshore from North Carolina to southeast Florida. In addition, gag in spawning condition were taken during research cruises documenting the occurrence of spawning north of Florida (off South Carolina and Georgia at depths ranging from 49 to 91 m).

Manuscript accepted 13 January 1998.
Fish. Bull. 96:797–807 (1998).

Changes in the sex ratio and size at maturity of gag, *Mycteroperca microlepis*, from the Atlantic coast of the southeastern United States during 1976–1995*

John C. McGovern

David M. Wyanski

Oleg Pashuk

Marine Resources Research Institute
South Carolina Department of Natural Resources
P.O. Box 12559, Charleston, South Carolina 29422-2559
E-mail address (for J.C. McGovern): mcgovernj@mrd.dnr.state.sc.us

Charles S. Manooch II

Southeast Fisheries Science Center
National Marine Fisheries Service, NOAA
Beaufort, North Carolina 28516-9722

George R. Sedberry

Marine Resources Research Institute
South Carolina Department of Natural Resources
P.O. Box 12559, Charleston, South Carolina 29422-2559

Gag, *Mycteroperca microlepis*, is a large, slow-growing serranid associated with inshore-reef and shelf-break habitats in the western Atlantic from New York to Brazil and in the Gulf of Mexico (Smith, 1971; Huntsman, 1976; Hardy, 1978; Collins et al., 1987). Gag are protogynous and probably make annual late-winter migrations to specific locations to form spawning aggregations (Collins et al., 1987; Keener et al., 1988; Van Sant et al., 1994). Recent evidence indicates that males may be selectively removed because they are the largest and most aggressive individuals in a spawning aggregation and are the first to be taken by fishing gear (Gilmore and Jones, 1992). Effects of fishing on spawning aggregations in other grouper species have been

found to be deleterious on population size, sex ratio, genetic diversity, and behavior of individuals (Nelson and Soulé, 1987; Smith et al., 1991; Carter et al., 1994; Coleman et al., 1996).

Histological examination of gonads of 498 gag collected throughout the year during 1976–82 along the southeast coast of the United States revealed that 84% were females, 15% males, and 1% were undergoing transition from female to male (Collins et al., 1987). Hood and Schlieder (1992) found similar sex ratios (14.0% male) for Gulf of Mexico gag collected from 1977 to

* Contribution 409 of the South Carolina Resources Center, South Carolina Department of Natural Resources, Charleston, SC 29422-2559.

1980. In both of these earlier studies, immature females were included in the sex ratio. In 1992, Coleman et al. (1996) determined that males made up a smaller percentage (1.9%) of the Gulf of Mexico adult (sexually mature) population than did males in the earlier study by Hood and Schlieder (1992). No current estimate of sex ratio is available for gag along the southeast coast of the United States.

In 1993, the South Atlantic Fishery Management Council (SAFMC) and the Florida Marine Fish Commission considered a closure for fishing of gag along the southeast coast during the gag spawning season to prevent the possibility that fishing on aggregations could severely decrease spawning output and affect sex ratios for future spawning seasons and generations (SAFMC, 1993). Much of the impetus for the proposed closure was the heavy fishing pressure exerted by recreational and commercial fishermen on spawning aggregations along the narrow Florida shelf. However, the SAFMC elected to take no action because it was unknown if gag spawned north of Florida and because the impacts of a spawning season closure for the entire southeast coast might be an unnecessary hardship on fishermen. In addition, no recent data were available on the sex ratio of gag along the southeast coast. Owing to the paucity of data on the current reproductive status of gag, the U.S. Department of Commerce followed recommendations from SAFMC and the National Marine Fisheries Service (NMFS) and enacted an emergency rule requiring all commercial vessels along the Atlantic coast of the southeastern United States to land gag in whole condition so that sex ratios and reproductive condition could be assessed. In this paper we compare current sex ratio and maturity data (1994–95) with historical information (1976–82). An additional objective of this work was to determine if gag spawn north of Florida.

Methods

Gag reproductive data were collected during 1976–82 and 1994–95 by the Marine Resources Monitoring Assessment and Prediction (MARMAP) program at South Carolina Department of Natural Resources (SCDNR). Data collected from 1976 to 1982 were obtained from the commercial hook and line fishery or research cruises conducted by the MARMAP program. These data (1976–82) were published by Collins et al. (1987), but raw data were available to us for comparison with recent information. During 1994–95, the collection of most gag resulted from an emergency rule that required commercial fishermen along the southeast Atlantic coast to land all gag with

gonads intact from 18 January through 18 April 1995. The rule was extended through 17 July 1995 but applied only to gag larger than 889 mm (TL). Upon reaching the dock, fishermen were instructed to contact a NMFS or state port sampler assigned to the region. The port samplers recorded date, port, approximate area of fishing, and total length (TL) and weight of specimens. All length measurements in our study refer to TL. Gonads were obtained from each specimen, packed in ice or preserved in formalin, and shipped to personnel of the MARMAP program. Additional samples were collected by MARMAP during 1994 and 1995 with chevron traps and hook-and-line gear at randomly chosen reef areas off the southeastern United States (Collins and Sedberry, 1991; Cuellar et al., 1996) and through port sampling efforts.

To assess sex and reproductive state, all gonads collected during 1994–95 were prepared for histological examination. The posterior portion of the gonad was removed and preserved in 10% formalin buffered with seawater. After a 2–6 week fixation, the tissue samples were transferred to 50% isopropanol, processed and vacuum infiltrated in a modular vacuum tissue processor, and blocked in paraffin. The resulting imbedded samples were sectioned at 7 μ m, stained with double-strength Gill hematoxylin, and counter-stained with eosin-y. A similar technique was used for the 1976–82 samples (Collins et al., 1987).

Sex and reproductive stage were assessed by one reader according to histological criteria (Table 1). Sections from 100 randomly selected specimens were examined by a second reader early in the study to verify the assessments. Specimens with developing, ripe, spent, or resting gonads were considered to be sexually mature. For females, this definition of sexual maturity included specimens with oocyte development at or beyond the cortical granule (alveoli) stage and specimens with beta, gamma, or delta stages of atresia. To ensure that females were correctly assigned to the immature and resting categories, the length-frequency histogram for immature females was compared to the histograms for resting females and females with evidence of certain maturity (e.g. developing, ripe, or spent). If there was little or no overlap between the two histograms representing mature individuals and the histogram for immature females, it was assumed that immature and resting individuals were not being confused.

To produce a sex ratio for the adult portion of the population, only data for mature gag were included in analyses. Data from Collins et al. (1987) and Hood and Schlieder (1992) were analyzed again to determine a sex ratio based on mature gag so that the results of these studies and the present study could

Table 1

Histological criteria used to determine reproductive state in gag, *Mycteroperca microlepis* (based on Moe, 1969; Hunter and Macewicz, 1985; Hunter et al. 1986; Collins et al., 1987; West, 1990; Ferreira, 1993; Shapiro et al., 1993a, 1993b).

Reproductive state	Male	Female
Immature	No primary males found. "Immature males" in Moe (1969) considered late transitional because sex transition is not yet completed.	No evidence of atresia. In comparison to resting female, oogonia more abundant along the margin of lamellae, most previtellogenic oocytes <80 μm in diameter, area of transverse section of ovary is smaller, lamellae lack muscle and connective tissue bundles, lamellae are not as elongate, and ovarian wall is thinner.
Developing	Development of cysts containing primary and secondary spermatocytes through some accumulation of spermatozoa in lobular lumina and peripheral sinuses within gonadal wall.	Oocytes undergoing cortical granule (alveoli) formation through nucleus migration and partial coalescence of yolk globules.
Running ripe	Predominance of spermatozoa in lobules and peripheral sinuses. Little or no occurrence of spermatogenesis.	Completion of yolk coalescence and hydration in the most advanced oocytes. Zona radiata becomes thin. Postovulatory follicles sometimes present.
Spent	No spermatogenesis. Some residual spermatozoa in lobules and peripheral sinuses.	More than 50% of vitellogenic oocytes in alpha or beta stage of atresia.
Resting	Little or no spermatocyte development. Empty lobules and sinuses evident.	Traces of atresia. In comparison to immature female, oogonia less abundant along margin of lamellae, most previtellogenic oocytes >80 μm in diameter, area of transverse section of ovary is larger, lamellae have muscle and connective tissue bundles, lamellae are more elongate and convoluted, and ovarian wall is thicker.
Developing, recent spawn	Not assessed.	Developing stage as described above plus presence of postovulatory follicles.
Mature specimen, state unknown	Mature, but inadequate quantity of tissue or postmortem histolysis prevent further assessment of reproductive state.	Mature, but inadequate quantity of tissue or postmortem histolysis prevents further assessment of reproductive state.

Transitional

Proliferation of spermatogonia through limited spermatogenesis within lamellae of resting ovary and development of peripheral sinuses in musculature of ovarian wall.

be compared. The sex ratio for 1995 was based on mature individuals that were collected during the early portion of the emergency rule (18 January to 18 April 1995). Recent data were analyzed by region: North Carolina, South Carolina, Georgia, northern Florida, and southern Florida (south of New Smyrna Beach). Plots of reproductive seasonality were based on all individuals that were collected during 1994 and 1995. Females that possessed hydrated oocytes or postovulatory follicles were considered to be in spawning condition.

Data for all females collected during the two periods were used in size-at-maturity analyses. The probit procedure (SAS, 1990) was used to fit a gompit model with the Gompertz distribution function to

maturity data in 5-cm-TL intervals. This procedure provided estimates of length at 50% maturity (L_{50}) and a comparison of size at maturity between periods. Analysis of variance (ANOVA) and the Duncan multiple range test were used to determine if there was a significant difference in the mean size of gag collected by month for mature individuals. ANOVA and the Duncan multiple range test were also used to determine if there was a significant difference in the monthly mean size of gag between 889 and 1050 mm TL to reduce the potential for bias that might result from selection of larger fishes during the latter part of the emergency rule. The results of all statistical tests were considered significant if P was <0.05.

Results

Histological examination of 2606 sexually mature gag (size range=517–1275 mm TL) taken during 18 January through 18 April 1995 revealed that there were significantly ($\chi^2=66.852$; $P<0.001$) fewer males (5.5%) along the southeast coast of the United States than during 1976–82 (19.6%; Tables 2 and 3). There were no significant differences in the percentage of males captured in 1995 off North Carolina, South Carolina, Georgia, and southern Florida ($\chi^2=4.926$; $P>0.05$; Table 4). However, the percentage of males taken in

northern Florida (14.9%) was significantly greater than in all other regions combined ($\chi^2=133.160$; $P<0.001$). Four collections accounted for over 35% of the males that were collected in northern Florida.

The size range of gag captured during 1994 and 1995 was similar to those caught from 1976 to 1982; however, there were some differences in size between periods for both sexes (Tables 3 and 5). Larger mature female gag were collected in 1994–95, although the mean lengths for the two periods were similar (1976–82: \bar{x} TL=831 mm, SD=92; 1994–95: \bar{x} TL = 832 mm, SD=82). The smallest mature female was

Table 2

Sex ratio of gag, *Mycteroperca microlepis*, (M=Male; F=Female; T=Transitional) taken during various studies in the northeast Gulf of Mexico and southeastern United States between 1976 and 1995. Sex ratios based on sexually mature individuals.

Study	Dates	Area	No. of M	% M	No. of F	% F	No. of T	% T
This study	1976–1982	SE Atlantic	104	19.6	419	78.9	8	1.5
Hood and Schlieder (1992)	1977–1980	NE Gulf of Mexico	125	15.6	659	82.5	15	1.9
Coleman et al. (1996)	1992	NE Gulf of Mexico	9	1.9	457	97.3	3	0.6
This study	18 Jan–18 April 1995 ¹	SE Atlantic	143	5.5	2468	94.4	2	0.1
This study	1994–1995	SE Atlantic	256	6.4	3720	92.7	39	0.9

¹ Period of emergency rule when fishermen were required to land all gag with gonads intact.

Table 3

Number of sexually mature gag, *Mycteroperca microlepis*, collected by size class during 1976–82 and 18 January to 18 April 1995 when fishermen were required to land all gag with intact gonads (TL=total length). Trans = transitional specimens.

Size (mm TL)	1976–1982			1995		
	Female	Male	Trans	Female	Male	Trans
450–499	—	—	—	—	—	—
500–549	2	—	—	2	—	—
550–599	1	—	—	12	—	—
600–649	10	—	—	19	—	—
650–699	14	—	—	79	—	—
700–749	31	—	—	171	—	—
750–799	64	1	2	437	—	—
800–849	94	1	1	709	—	1
850–899	79	1	2	580	5	1
900–949	42	4	1	271	3	—
950–999	7	13	1	99	26	—
1000–1049	13	14	—	48	48	—
1050–1099	5	27	—	27	36	—
1100–1149	—	14	—	6	13	—
1150–1199	—	2	—	1	7	—
1200–1249	—	1	—	—	5	—
1250–1299	—	—	—	—	—	—
No length	47	25	1	7	—	—
Total	419	104	8	2468	143	2
Percent	78.9	19.6	1.5	94.4	5.5	0.1

Table 4

Number of sexually mature gag, *Mycteroperca microlepis*, females (F), males (M), and transitionals (T) taken in North Carolina, South Carolina, Georgia, northern Florida, and southern Florida during 18 January to 18 April 1995 when fishermen were required to land all gag with intact gonads (TL=total length).

Size (mm TL)	North Carolina			South Carolina			Georgia			North Florida			South Florida		
	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
450-499	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
500-549	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—
550-599	1	—	—	10	—	—	—	—	—	1	—	—	—	—	—
600-649	3	—	—	12	—	—	1	—	—	—	—	—	3	—	—
650-699	13	—	—	39	—	—	16	—	—	4	—	—	7	—	—
700-749	37	—	—	87	—	—	35	—	—	6	—	—	6	—	—
750-799	53	—	—	199	—	—	113	—	—	46	—	—	26	—	—
800-849	64	—	—	234	—	1	214	—	—	111	—	—	86	—	—
850-899	64	—	—	160	3	—	148	1	—	155	—	—	53	1	1
900-949	23	—	—	66	1	—	43	1	—	112	—	—	27	1	—
950-999	19	1	—	11	3	—	16	1	—	44	18	—	9	3	—
1000-1049	7	3	—	4	5	—	10	4	—	26	33	—	1	3	—
1050-1099	3	1	—	2	4	—	7	3	—	14	27	—	1	1	—
1100-1149	—	—	—	3	1	—	—	1	—	2	9	—	1	2	—
1150-1199	—	—	—	—	3	—	1	1	—	—	3	—	—	—	—
1200-1249	—	1	—	—	1	—	—	2	—	—	1	—	—	—	—
1250-1299	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
No lengths	—	—	—	2	—	—	2	—	—	2	—	—	1	—	—
Total	287	6	—	831	21	1	606	14	—	523	91	—	221	11	1
Percent	97.9	2.1	—	97.4	2.5	0.1	97.7	2.3	—	85.1	14.9	—	94.8	4.7	0.5

508 mm in 1976-82 and 517 mm in 1994-95. All gag >683 mm in the 1976-82 samples and those >750 mm in the 1994-95 samples were sexually mature. During 1994-95, 266 males (\bar{x} TL=1041 mm, SD=68) were collected and no gag less than 875 mm was male (Table 5). During 1976-82, 104 males (\bar{x} TL=1041 mm, SD=73) were collected with the smallest specimen at 795 mm. The transitional specimens collected during 1994-95 were larger than those from 1976 to 1982.

The length at 50% maturity (L_{50}) was similar during 1978-82 (641 mm; 95% confidence interval (CI) =616-658 mm) and 1994-95 (622 mm; 95% CI=611-631 mm (Fig. 1); however, the probit analysis with period and total length as independent variables (Pearson χ^2 , $P=0.9953$, $df=27$) indicated that the size at maturity was likely decreasing (Table 6). The negative coefficient for period indicated that overall a smaller proportion of specimens in each size class was mature during 1976-82. The overlap in the histograms of female gag that were developing, ripe, or spent and females that were resting indicated that reproductive tissue was correctly assigned to the immature and resting categories (Fig. 2).

Female gag were in spawning condition from December 1994 through mid May 1995 on the basis of

Table 5

Number of mature gag, *Mycteroperca microlepis*, taken during 1994-95 (TL=total length). Trans = transitional specimens.

Size (mm TL)	Female	Male	Trans
450-499	0	—	—
500-549	2	—	—
550-599	16	—	—
600-649	35	—	—
650-699	121	—	—
700-749	267	—	—
750-799	650	—	1
800-849	1021	—	2
850-899	790	7	5
900-949	386	14	12
950-999	132	46	10
1000-1049	70	82	8
1050-1099	33	68	—
1100-1149	7	28	—
1150-1199	2	15	—
1200-1249	—	5	1
1250-1299	1	—	—
No Lengths	41	1	—
Total	3574	266	39
Percent	92.1	6.9	1.0

occurrence of hydrated oocytes or postovulatory follicles (Fig. 3). Spawning individuals were caught from North Carolina to Florida by commercial fishermen and fishery-independent sampling (MARMAP). Approximate fishing locations provided by commercial fishermen indicated that gag were spawning from the border between North Carolina and South Carolina to a point east of Ft. Lauderdale, Florida. Spawning individuals were captured on research cruises off South Carolina and Georgia at depths ranging from 49 to 91 m. The spawning season appeared to be more protracted in southern Florida than in other areas, with spawning beginning in December and extending into mid May. Peak spawning occurred from March through mid-April (Fig. 4). When the data were stratified by area, the highest percentage of spawning females was found in northern Florida during March and April (Fig. 4).

Overall, spawning of gag declined rapidly after 8 April. Individuals undergoing sexual transition were extremely rare during most of the spawning season; only one transitional specimen was documented during February and March 1994–95, out of 2147 fish examined (Table 7). There was a sharp increase in the number of transitional individuals immediately after the spawning season. The majority of transitional fish ($n=26$) were collected during mid-April through mid-June when 1473 gag gonads were ex-

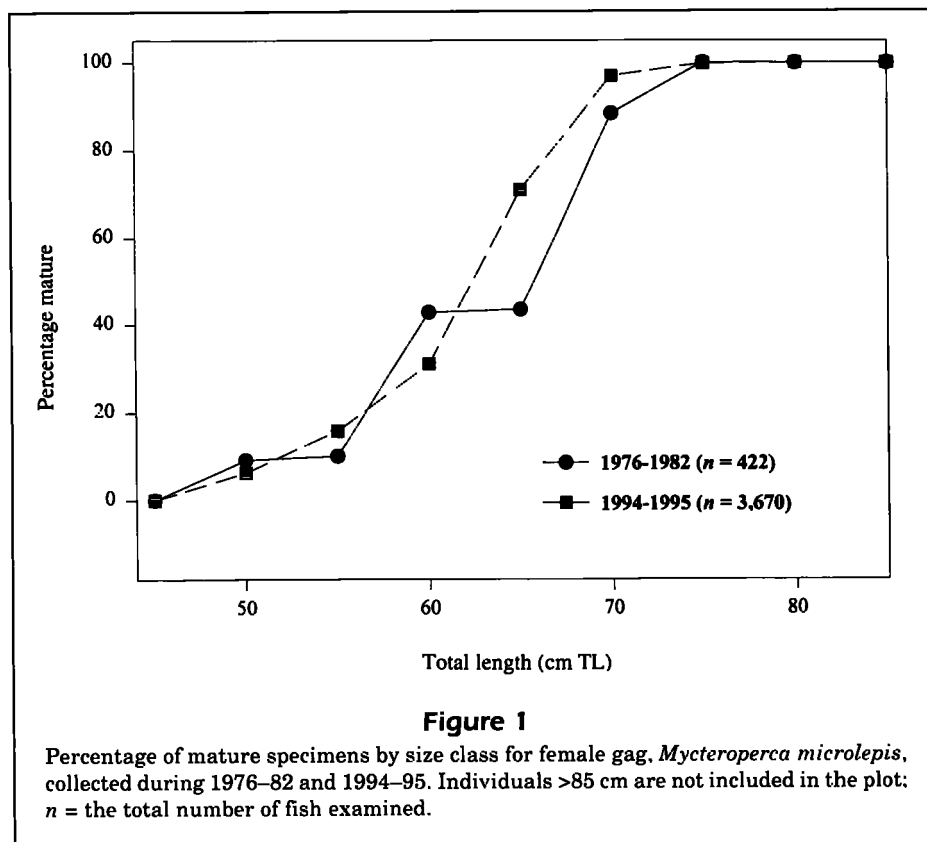


Figure 1

Percentage of mature specimens by size class for female gag, *Mycteroperca microlepis*, collected during 1976–82 and 1994–95. Individuals >85 cm are not included in the plot; n = the total number of fish examined.

amined. ANOVA and the Duncan multiple range tests indicated that there were significant differences in the mean lengths of gag sampled between months. When the number of males, females, and transitionals between 889 mm and 1050 mm was tabulated

Table 6

Results of probit analysis comparing the proportions of mature females in 5-cm length intervals collected during two periods: 1976–82 and 1994–95 (TL=total length).

Parameter	Estimate	SE	P
Intercept	-12.304	0.871	<0.0001**
Period	-0.378	0.176	0.0320*
cm TL	0.192	0.013	<0.0001**

* = significant at $P<0.05$; ** = significant at $P<0.0001$.

Table 7

Total number sampled (n), mean total length (mm TL; sexes combined), standard deviation (SD), number of males (M), number of females (F), and number of transitional specimens (T) by month for mature gag captured during 1994 and 1995. Means with same letter are not significantly different ($P>0.05$).

Month	n	\bar{x} TL	SD	M	F	T
Jan	243	837.0 ^{bcd}	85.5	10	229	4
Feb	754	829.7 ^{bcd}	87.0	27	726	1
Mar	1142	859.0 ^b	99.2	87	1055	—
Apr	1027	844.8 ^{bc}	86.4	50	965	12
May	297	873.2 ^{ab}	110.8	48	235	14
Jun	48	928.1 ^a	110.7	11	32	5
Jul	77	925.9 ^a	124.1	19	56	2
Aug	2	717.0 ^f	106.1	—	2	—
Sep	33	774.8 ^{ef}	84.1	2	31	—
Oct	24	759.7 ^{ef}	83.6	—	24	—
Nov	77	818.5 ^{de}	86.8	—	76	—
Dec	89	788.5 ^{cde}	89.7	2	86	1

to reduce the potential for bias that might result from the selection of larger fishes after 18 April 1995, the Duncan multiple range test showed little difference in the mean size of gag collected each month (Table 8), and it was still apparent that transitional fish did not appear in the collections until immediately after the spawning season.

Discussion

Analysis of reproductive data indicates that the gag population along the southeast coast of the United States is stressed. The percentage of males in the adult population has decreased from 19.6% (1976–82) to 5.5% (1994–95). However, the percentage of males currently in the population may actually be less than 5.5%; more recent data were collected during the spawning season when male gag are most vulnerable to fishing gear (Coleman et al., 1996). In contrast, data were collected throughout the year during 1976–82 rather than primarily during the spawning season. Had the 1995 emergency rule been put into place at a time of the year when gag were not spawning, it is possible that fewer males would have been captured.

The relative abundance of males and the length of the spawning period were greater off Florida than off other southeastern states. The highest percentage of males (14.9%) during 1995 was noted off northern Florida. However, the majority of males were taken by one fisherman on 2 March 1995, 17 March 1995, and 1 April 1995 indicating that this fisherman may have been targeting a relatively unfished spawning aggregation. Spawning aggregations of gag (Coleman et al., 1996) and red hind, *Epinephelus guttatus* (Shapiro et al., 1993a), contained a higher percentage of males than nonaggregation groups. Commercial fishermen indicate that after the spawning season (May and June), female gag move in groups to shallower water (~30 m) and the larger males become solitary and remain at depths of 50 to 90 m.

Probit analysis revealed that female gag may have been maturing at smaller sizes during 1994–95 than during 1976–82 which would further indicate that

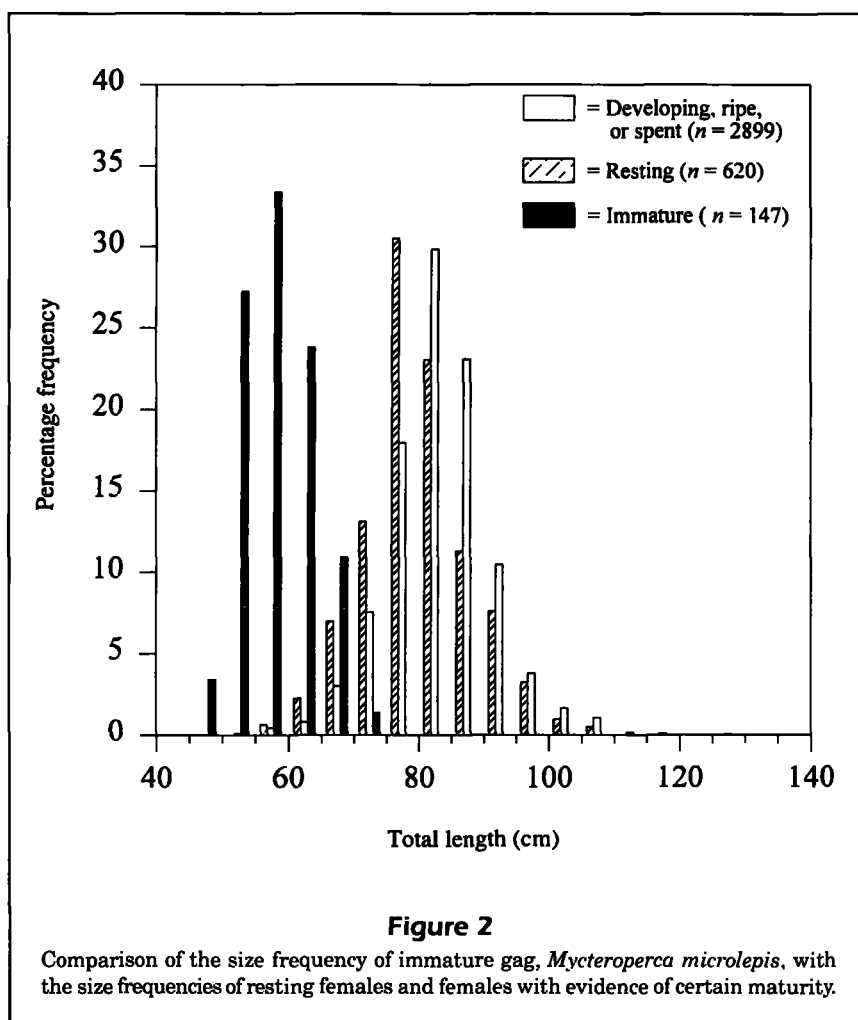
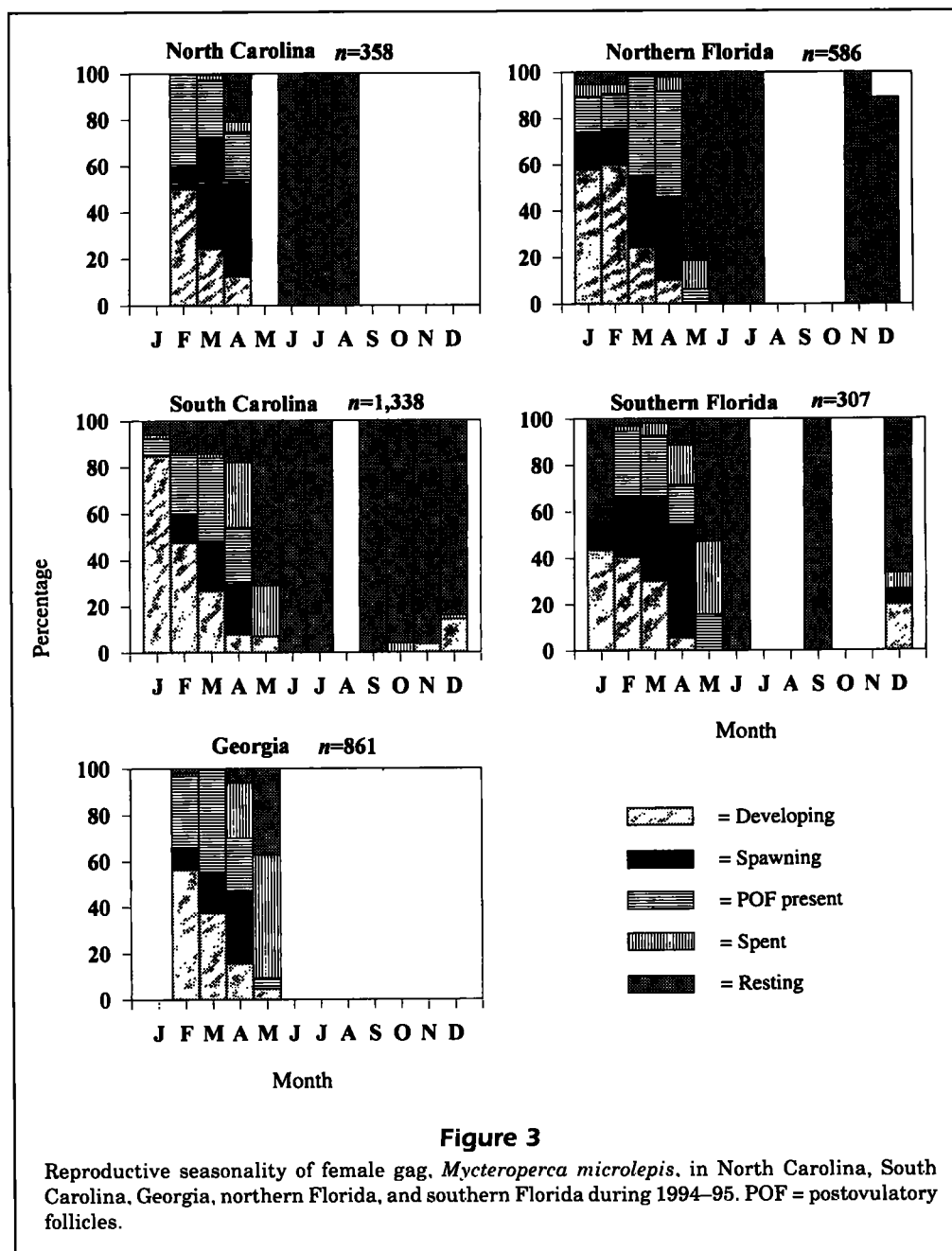


Table 8

Total number sampled (n), mean total length (mm TL; sexes combined), standard deviation (SD), number of males (M), number of females (F), and number of transitional specimens (T) by month for mature gag (>889 mm and <1050 mm) captured during 1994 and 1995. Means with same letter are not significantly different ($P > 0.05$).

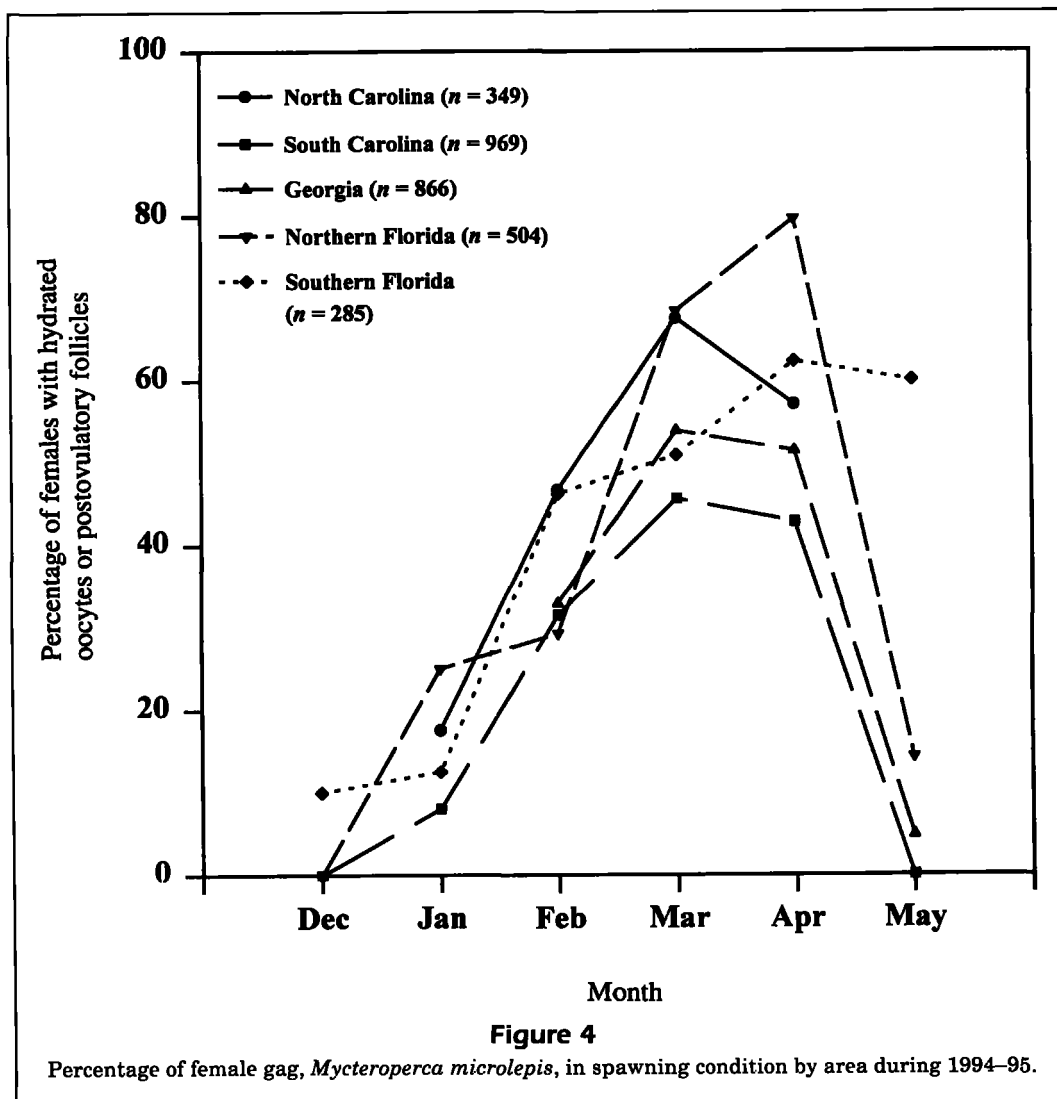
Month	n	\bar{x} TL	SD	M	F	T
Jan	45	932.4 ^b	41.5	5	38	2
Feb	126	935.6 ^b	42.5	12	114	—
Mar	308	948.3 ^{ab}	46.4	51	257	—
Apr	219	939.6 ^{ab}	43.8	27	183	9
May	92	949.8 ^{ab}	43.4	24	54	14
Jun	25	971.0 ^{ab}	49.7	7	13	5
Jul	41	963.1 ^{ab}	46.7	10	30	1
Aug	0	—	—	—	—	—
Sep	3	986.7 ^a	28.9	2	1	—
Oct	2	944.5 ^{ab}	77.1	—	2	—
Nov	10	961.6 ^{ab}	52.7	1	9	—
Dec	11	933.0 ^b	47.4	2	8	1



the gag population is stressed. Although probit analysis suggested size at maturity is decreasing, it is difficult to conclude that this is happening in the population on the basis of estimates of L_{50} because there is overlap in the confidence intervals. A cautious interpretation is also warranted given the small number of females ($n=422$) sampled during 1976–82. Coleman et al. (1996) found that female gag collected in the Gulf of Mexico during 1991–93 became sexually mature and underwent transition at smaller sizes than those reported by Hood and Schlieder (1992) for the same region during 1977–80. Changes

in life history aspects of gag from the Gulf of Mexico were attributed to steadily increasing fishing pressure.

Gag were in spawning condition from December through mid May in southern Florida, January through May in northern Florida, and January through April in South Carolina. Although no specimens were collected during January in North Carolina and Georgia, individuals in spawning condition were landed during February through April. Peak spawning activity occurred from March through mid-April in all areas. Collins et al. (1987) and Keener et al. (1988) also reported that peak spawning occurred



in March and April along the southeast Atlantic coast. Hood and Schlieder (1992) and Coleman et al. (1996) indicated that peak spawning occurred during February and March in the Gulf of Mexico.

Despite the large number of specimens examined during 1994-95 ($n=3879$), transitional specimens ($n=39$) made up a small percentage (1.0%) of individuals collected. The low number of individuals with transitional gonads may have been due to the rapid nature of sex transition that appears to occur immediately after the spawning season. Smith (1965) and Moe (1969) suggested that other groupers may have a quick rate of sex transition. Because there was no significant monthly difference in the mean length of gag between 889 and 1050 mm TL landed during January through July, we feel that the peak in the number of transitional specimens during April and May was real and not an artifact of the emergency rule that required fishermen to land only larger fish

(>889 mm TL) after 18 April. Coleman et al. (1996) stated that sex transition in gag and other grouper species may be socially mediated either through size ratio or sex ratio cues. Shapiro et al. (1993b) proposed that one function of annual spawning aggregations in red hind may be that of enabling a female to determine if it should function as a female or a male during the next spawning season. Shapiro et al. (1993b) further suggested that if this hypothesis is true, sex-changing individuals should be found soon after the aggregation has dispersed. The high percentage of males and transitionals taken during April and May in this study indicates that aggregations may remain intact for a short time after the spawning season.

Van Sant et al. (1994) and MARMAP tagging data¹ provided evidence that some gag migrate from off-

¹ 1998. Unpublished data from MARMAP tagging study. Marine Resources Research Institute, Charleston, SC.

shore areas of South Carolina and Georgia to the shelf edge off Florida, perhaps to spawn. However, the presence of hydrated oocytes and new postovulatory follicles in female gag taken from North Carolina through Florida, including specific locations off South Carolina and Georgia, shows that spawning is not restricted to Florida. Hunter et al. (1985) reported that the presence of hydrated oocytes in teleosts is an indication that individuals will spawn within 12 hours. Furthermore, Hunter et al. (1986) found that postovulatory follicles are present only in fishes that have recently spawned.

Gag off Florida are subject to intense fishing pressure by commercial fishermen, sport divers, and anglers, particularly during the late fall through early spring, because the continental shelf is very narrow and spawning aggregations are easily accessed. Therefore, even if most gag are not migrating to Florida for spawning, the vulnerability of at least part of the stock to winter fishing is of concern. This "funneling" of migratory fishes off southeastern Florida may increase fishing mortality for many species and requires further investigation.

In 1993, the SAFMC decided to take no action on a proposal to close all fishing for gag during their spawning season because insufficient data were available on sex ratios and the spatial extent of spawning along the southeast coast of the United States. The information on sex ratio and size at maturity presented here indicates that the gag population is overfished. Because there has been a reduction in the percentage of males in commercial landings and a modest decrease in the size at maturity for females, the total fishing effort should be limited, especially in the removal of males from spawning aggregations. Since gag spawn in offshore areas from North Carolina to southeast Florida, any regulation should apply to all southeastern states. However, seasonal closure to fishing may not be sufficient to protect gag from overexploitation because males will continue to be lost during the open season. Protected areas with no fishing, such as marine fishery reserves, may be a possible solution to overfishing of reef fishes along the southeast coast of the United States (PDT, 1990). Marine fishery reserves can protect population age structure, species diversity, genetic diversity, and recruitment supply to exploited areas (Bohnsack, 1993). Sedberry et al. (1996) found that marine reserves in Belize, Central America, had a higher diversity of fishes than in areas that were not protected. Top predators, such as various grouper and snapper species, were more abundant and larger in reserves. In addition, populations of herbivorous forage species were reduced to presumed natural levels in the presence of pro-

tected predators. Marine reserves in Belize appear to have a natural balance of predators and forage species in relation to fished areas. There are other species in the snapper-grouper complex that are showing signs of overfishing, in addition to gag, including red porgy (Harris and McGovern, 1997), vermilion snapper (Zhao and McGovern, 1997; Zhao et al., 1997), and black sea bass.² In addition, less important species in fisheries (e.g. white grunt, gray triggerfish) are increasing in abundance.² This trend is likely to continue unless different management regulations are imposed that will protect ecosystems and restore a natural equilibrium community.

Acknowledgments

We thank personnel associated with cooperative state and federal agencies, for their assistance with the collection of data, and commercial fishermen for providing trip information. In particular, we recognize T. Brandt, L. Bishop, M. Burton, D. Codella, C. Dennis, R. Roman, and D. Thiesen of the NMFS, G. Rogers and J. Ross of the Georgia Department of Natural Resources, and F. Rohde of the North Carolina Department of Environment, Health, and Natural Resources for their efforts. We thank Dr. John Grego (University of South Carolina) for helping us with the probit procedure. The assistance at sea by SCDNR MARMAP personnel and the crew of the RV *Palmetto* is appreciated. We also thank K. Grimball, T. Kellison, and other MARMAP personnel for processing gonads that were sent from state and federal port samplers. This study was sponsored by the National Marine Fisheries Service (MARMAP Contract No. 52WCNF6006013PW and Saltonstall-Kennedy Grant NA57FD0030), and the South Carolina Department of Natural Resources.

Literature cited

- Bohnsack, J. A.**
 1993. Marine reserves. *Oceanus* 36:63-71.
- Carter, J., G. J. Marrow, and V. Pryor.**
 1994. Aspects of the ecology and reproduction of Nassau grouper, *Epinephelus striatus*, off the coast of Belize, Central America. *Proc. Gulf Caribb. Fish. Inst.* 43:65-111.
- Coleman, F. C., C. C. Koenig, L. A. Collins.**
 1996. Reproductive styles of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. *Environ. Biol. Fish.* 47:129-141.

² 1998. MARMAP unpublished data. Marine Resources Research Institute, South Carolina Department of Natural Resources, Charleston, SC 29422-2559.

- Collins, M. R., and G. R. Sedberry.**
1991. Status of vermilion snapper and red porgy stocks off South Carolina. *Trans. Am. Fish. Soc.* 120:116–120.
- Collins, M. R., C. A. Waltz, W. A. Roumillat, and D. L. Stubbs.**
1987. Contribution to the life history and reproductive biology of gag, *Mycteroperca microlepis* (Serranidae), in the South Atlantic Bight. *Fish. Bull.* 85:648–653.
- Cuellar, N., G. R. Sedberry, and D. M. Wyanski.**
1996. Reproductive seasonality, maturation, fecundity, and spawning frequency of the vermilion snapper, *Rhomboplites aurorubens*, off the southeastern United States. *Fish. Bull.* 94:635–653.
- Ferreira, B. P.**
1993. Reproduction of the inshore coral trout *Plectropomus maculatus* (Perciformes: Serranidae) from the Central Great Barrier Reef, Australia. *J. Fish. Biol.* 42:831–834.
- Gilmore, R. G., and R. S. Jones.**
1992. Color variation and associated behavior in the epinepheline groupers, *Mycteroperca microlepis*, (Goode and Bean) and *M. phenax* Jordan and Swain. *Bull. Mar. Sci.* 51:83–103.
- Hardy, J. E., Jr.**
1978. Development of fishes of the Mid-Atlantic Bight—an atlas of egg, larval, and juvenile stages, vol. III: Aphredoderidae through Rachycentridae. U.S. Fish and Wildl. Serv., U.S. Dep. Interior, 394 p.
- Harris, P. J. and J. C. McGovern.**
1997. Changes in the life history of red porgy, *Pagrus pagrus*, from the southeastern United States, 1972–1994. *Fish. Bull.* 95:732–747.
- Hood, P. B., and R. A. Schlieder.**
1992. Age, growth, and reproduction of gag *Mycteroperca microlepis*. (Pisces: Serranidae), in the eastern Gulf of Mexico. *Bull. Mar. Sci.* 51:337–352.
- Hunter, J. R., N. C. H. Lo, and R. J. H. Leong.**
1985. Batch fecundity in multiple spawning fishes. In R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*), p. 67–77. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36.
- Hunter, J. R., and B. J. Macewicz.**
1985. Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax*. *Fish. Bull.* 83:119–136.
- Hunter, J. R., B. J. Macewicz, and J. R. Sibert.**
1986. The spawning frequency of skipjack tuna, *Katsuwonus pelamis*, from the South Pacific. *Fish. Bull.* 84:895–903.
- Huntsman, G. R.**
1976. Offshore headboat fishing in North Carolina and South Carolina. *Mar. Fish. Rev.* 38(3):13–23.
- Keener, P., G. D. Johnson, B. W. Stender, E. B. Brothers and H. R. Beatty.**
1988. Ingress of postlarval gag, *Mycteroperca microlepis* (Pisces: Serranidae), through a South Carolina barrier island inlet. *Bull. Mar. Sci.* 42:376–396.
- Moe, M. A., Jr.**
1969. Biology of the red grouper, *Epinephelus morio* (Valenciennes), from the eastern Gulf of Mexico. Fla. Dep. Nat. Resour. Mar. Res. Lab., Prof. Pap. 10, 95 p.
- Nelson, K., and M. Soulé.**
1987. Genetic conservation of exploited fishes. In N. Ryman and F. Utter (eds.), Population genetics and fishery management, p. 345–368. Univ. Washington Press, Seattle, WA.
- PDT (Snapper-Grouper Plan Development Team).**
1990. The potential of marine fishery reserves for reef fish management in the U.S. South Atlantic. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SEFC-216, 45 p.
- SAFMC (South Atlantic Fishery Management Council).**
1993. Amendment number 6, regulatory impact review and final environmental impact statement for the snapper grouper fishery of the South Atlantic region. SAFMC, Charleston, SC, 189 p.
- SAS Institute, Inc.**
1990. SAS/STAT® user's guide, version 6, 4th edition, vol. 2. SAS Institute, Inc, Cary, North Carolina, p. 1325–1350.
- Sedberry, G. R., J. Carter and P. A. Barrick.**
1996. A comparison of fish communities between protected and non-protected areas of the Belize Barrier Reef ecosystem: Implications for conservation and management. *Proc. Gulf Caribb. Fish. Inst.* 45:95–127.
- Shapiro, D. Y., Y. Sadovy, and M. A. McGehee.**
1993a. Periodicity of sex change and reproduction in the red hind, *Epinephelus guttatus*, a protogynous grouper. *Bull. Mar. Sci.* 53:1151–1162.
1993b. Size, composition, and spatial structure of the annual spawning aggregation of the red hind, *Epinephelus guttatus* (Pisces: Serranidae). *Copeia* 1993:399–406.
- Smith, C. L.**
1965. The patterns of sexuality and the classification of serranid fishes. *Am. Mus. Novit.* 2207:1–20.
1971. A revision of American groupers: *Epinephelus* and allied genera. *Bull. Am. Mus. Nat. Hist.* 146:67–242.
- Smith, P. J., R. I. C. C. Francis, and M. McVeagh.**
1991. Loss of genetic variation due to fishing pressure. *Fish. Res.* 10:309–316.
- West, G.**
1990. Methods of assessing ovarian development in fishes: a review. *Aust. J. Mar. Freshwater Res.* 41:199–222.
- Van Sant, S. B., M. R. Collins, and G. R. Sedberry.**
1994. Preliminary evidence from a tagging study for a gag (*Mycteroperca microlepis*) spawning migration, with notes on the use of oxytetracycline for chemical tagging. *Proc. Gulf Caribb. Fish. Inst.* 43:417–428.
- Zhao, B., and J. C. McGovern.**
1997. Temporal variation in sexual maturity and gear-specific sex ratio of the vermilion snapper in the South Atlantic Bight. *Fish. Bull.* 95:837–848.
- Zhao, B., J. C. McGovern, and P. J. Harris.**
1997. Age, growth, and temporal change in size at age of the vermilion snapper from the South Atlantic Bight. *Trans. Am. Fish. Soc.* 126:181–193.