Reproductive patterns, sex ratio, and fecundity in gag, *Mycteroperca microlepis* (Serranidae), a protogynous grouper from the northeastern Gulf of Mexico

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Abstract.—We determined sex ratio, spawning season, batch fecundity, spawning frequency, and annual fecundity for gag (Serranidae: *Mycteroperca microlepis*), a protogynous hermaphrodite. Gag were randomly sampled from 1991 through 1993 (n=1398) and selectively sampled with a bias towards heavily pigmented fish in 1994 (n=648). All samples were taken from commercial and recreational fisheries in the northeastern Gulf of Mexico. Sex ratio was 49 females:1 male for the 1991–93 samples. Heavily pigmented gag (n=62), commonly thought to be males, were collected from waters >41.0 m during all months except January and March. Of these, 60 were histologically sexed and found to be 5.0% female, 3.3% possibly early transitional male, and 91.7% male. Indeterminate spawning generally occurred from February through April in water depths >30.5 m. Hydrated oocytes were homogeneously distributed in hydrated ovaries. Shortest length and youngest age at spawning were 577 mm total length (TL) and 3 years for females, and 981 mm TL and 8 years for males. The highest batch fecundity (865,295 hydrated oocytes) occurred in an 8-year-old, 1038-mm-TL gag. Batch fecundity had a significant (α=0.01) positive correlation with TL, gutted body weight, and age but was most strongly correlated with TL. Average annual spawning frequency ranged from 8 to 27 for 2- to 9-year-old fish, varying significantly by year (P<0.05) and among years and age classes (P<0.02). Annual fecundity estimates ranged from 0.065 to 61.4 million and correlated well with age.

Manuscript accepted 25 November 1997.
Fishery Bulletin 96:415–427 (1998).

The spawning potential ratio (SPR), which is used to estimate the adult stock size as a percentage of the unfished stock, is an important assessment tool in the management of fish stocks (Goodyear, 1993). An accurate determination of SPR requires a basic understanding of reproduction (Huntsman and Schaaf, 1994), including information on sex ratio, spawning season duration, and size (and age) at first spawning, as well as estimates of batch fecundity, spawning frequency, and annual fecundity by fish size.

Gag (Serranidae: *Mycteroperca microlepis*), a large, economically important, shallow-water grouper found from Massachusetts to Rio de Janeiro, Brazil, (Briggs, 1958) is heavily fished in the Gulf of Mexico on Florida's western shelf, with 1986–92 annual commercial landings of about 6.80×10^5 kg (1.5 million lb) and recreational landings of 0.2–0.6 million fish (Gulf of Mexico Fishery Management Council[1]; Schirripa and Goodyear[2]). The gag is a winter-spring spawning, monandric protogynous hermaphrodite that matures sexually around 550 mm total length and 3 to 6 yr (McErlean and Smith, 1964; Collins et al., 1987; Bullock and Smith, 1991; Hood and Schlieder, 1992; Coleman et al., 1996; Koenig et al., 1996). Gilmore and Jones (1992), who described the reproductive behavior and color variation of gag off the east coast of Florida, assumed that large gag with heavy pigmentation ("black-belly" and "black-back") were males. Similarly, Bullock and Smith (1991) assumed that large gag "with dark pigmentation ventrally" from the Gulf of Mexico were male. More recently, Koenig et al. (1996) and Coleman et al. (1996) have described reproductive styles of gag and the apparent effects of fishing on gag spawning aggregations.

Although these studies (above) have examined some aspects of gag reproduction, few have addressed

[1] Gulf of Mexico Fishery Management Council. 1989. Amendment number 1 to the reef fish fishery management plan. GMFMC, Tampa, Florida, 356 p.

[2] Schirripa, M. J., and C. P. Goodyear. 1994. Status of the gag stocks of the Gulf of Mexico: assessment 1.0. Miami Laboratory, Natl. Mar. Fish. Serv., NOAA, 75 Virginia Beach Drive, Miami, FL 33149.

either fecundity or spawning frequency, and none have used the methods developed by Hunter et al. (1985) for multiple-spawning fishes. Hunter's methods have been used successfully to estimate batch fecundity, spawning frequency, and annual fecundity in other Gulf of Mexico fishes similar to gag in size and longevity (e.g. Fitzhugh et al., 1988; Taylor and Murphy, 1992; Render and Wilson, 1992; Fitzhugh et al., 1993; Nieland and Wilson, 1993; Wilson and Nieland, 1994; and Collins et al., 1996). Such estimates obtained with these newer methods are far more accurate than the previously used "ovarian egg number" methods for multiple spawning fishes (as described in Hunter et al., 1985).

In this study, we estimate sex ratio, spawning season duration, length and age at first spawning, depth of spawning, batch fecundity, spawning frequency by year, spawning frequency by size and age, and annual fecundity in gag from the Gulf of Mexico. We also test the assumption that heavily pigmented gag represent only males using histological examination of gonads of heavily pigmented fish.

Methods

Gag were randomly sampled from commercial and recreational landings from Panama City to St. Petersburg, Florida, in 1991, 1992, and 1993. In 1994, we asked commercial fishermen to leave all heavily pigmented gag ungutted so that they could be examined for sex. Gag were considered heavily pigmented only if they retained the heavy-black pigment on the ventral portion of the abdomen after death (e.g. plate XVI, Fig. D., page 237, in Bullock and Smith, 1991). Total length (TL, in mm), fork length (FL, in mm), and total (ungutted) weight (TW, in g) were recorded before removing gonads, which were kept on ice prior to examination.

Gonads of reproductively active gag are so large that they require subsampling for determination of sex. To ensure that a single tissue sample per female would be adequate to estimate maximum oocyte diameter and hydrated oocyte counts, we first tested for tissue homogeneity. To test for homogeneity of oocyte diameter, three bilobed ovaries with hydrated oocytes were divided into six equal sections (three from each lobe) and subsampled to determine the frequency distributions of oocyte diameters; they were tested for homogeneity with a Kolmogorov-Smirnov two-sample test (Sokal and Rohlf, 1981). To test for homogeneity of density of hydrated oocytes, we used six hydrated ovaries divided in the same manner and determined the number of hydrated oocytes per gram; samples were tested for homogeneity with a two-way ANOVA (SAS, 1988).

We made a preliminary determination of sex in gag using fresh, unstained samples. A small sample was removed from each gonad, teased apart, and viewed microscopically (250×). Sex was assigned according to the following criteria: females had oocytes and no tissues that could be mistaken for spermatogenic tissue; males had no oocytes (or few small oocyte remnants); and transitional males had high numbers of oocytes and possible sperm (Shapiro et al., 1993).

Female gonads were then microscopically staged. Maximum oocyte diameter (MOD) was recorded; the most advanced oocyte type present was noted and used to assign individuals to one of five ovarian-maturation stages: 1) mature, resting (MOD<0.12 mm and clear); 2) early developing (MOD<0.20 mm and slightly opaque); 3) late developing (MOD=0.20 to 0.59 mm and opaque); 4) ripe (MOD>0.59 mm and mostly transparent); and 5) spent (much loose particulate matter in flaccid ovary) (West, 1990). After fat and mesentery were removed, gonads were blotted dry, weighed to the nearest 0.1 g., and placed in 10% buffered formaldehyde solution.

We then selected and prepared some of the gonad samples (above) to verify sex and stage using standard histological techniques. Five-µm-thick sections were prepared from tissues embedded in paraffin and stained with Harris's hematoxylin and eosin. Ovarian stages were assigned on the basis of the most advanced oocyte or follicle stage present: 1) primary growth; 2) cortical alveolar; 3) vitellogenic; 4) hydrated; and 5) spent (presence of postovulatory follicles [POFs]). Stages 1–4 followed Wallace and Selman (1981). Histological stages of possible early transitional males and functional males were as follows: 6) possible early transitional males had active female tissue with possible crypts containing primary spermatocytes (Moe, 1969; Johnson, 1995); 7) mature inactive males had a few secondary spermatocytes and remnant oocytes (primary growth and atretic only); 8) mature active males had many secondary spermatocytes and remnant oocytes; 9) ripening males had spermatids in ducts; and 10) ripe males had tailed spermatozoa in ducts. Sex and stage were compared by gonad-region for all heavily pigmented gag. Physical condition of the gonad (e.g. intactness, presence of parasites, possible preservation problems) was also noted.

We estimated duration of the spawning season by using two techniques: 1) plotting gonadosomatic index (GSI=gonad weight (100)/TW) by month for all gag with gonads in good condition (≥90% intact) and 2) determining when hydrated ovaries with nondegenerated POFs appeared. Proof of actual spawning (and not just the presence of "ripe" ovaries, as discussed in Sadovy et al., 1994) was provided by

POFs. Size and age at first spawning, and water depth of spawning, were determined with only histological stage-4 females and stage-10 males. Depth of spawning was indicated by depth of catch, as determined from interviews with fishermen.

Batch fecundity estimates involved counting whole, hydrated oocytes taken from cross sections of gonads and weighed (to the nearest 0.001 g) following Hunter et al. (1985). Samples were examined histologically for the presence of POFs and hydrated oocytes. The POFs in samples were noted as 0 (absent), 1 (degenerating), or 2 (nondegenerating) (Fitzhugh and Hettler, 1995). Ovaries with nondegenerating POFs were omitted from batch fecundity estimates to avoid biases in determining the number of hydrated oocytes per gram of tissue (Hunter et al., 1985). Batch fecundity estimates were calculated by dividing the product of gonad weight and number of hydrated oocytes by the sample weight. Any fish collected late in the spawning season were omitted from batch fecundity analyses because of apparent decreases in batch size (e.g. Fitzhugh et al., 1988).

Spawning frequency (the number of spawnings per year by a female) was estimated by dividing the duration of the spawning season by the average number of days between spawning for all females (Hunter and Macewicz, 1985; Hunter et al., 1986). Duration of the spawning season was the number of days between the first and last occurrence of hydrated oocytes or POFs each year. The average number of days between spawning for all females (> or = TL of the smallest hydrated fish) was 100% divided by the percentage frequency of hydrated females. For example, if the spawning season was 100 days long and females spawned every two days (with 50% hydrated), then spawning frequency would be 50.

We obtained annual fecundity estimates by multiplying batch fecundity by spawning frequency. Age-dependent spawning frequency was estimated with stage-4 females within each age group. Because spawning frequency varied by age and year, these variables were considered separately in calculating annual fecundity. We analyzed the following relationships using regression: batch fecundity (*BF*) × *TL*, *BF* × *age*, and *BF* × *gutted body weight* (*GBW=total weight – gonad weight = TW – GW*); *spawning frequency* × *age*; *annual fecundity* (*AF*) × *TL*, *AF* × *age*, and *AF* × *GBW*.

Most fish were aged by using whole or sectioned sagittal otoliths (Johnson et al., 1993). Whole otoliths were adequate for ageing smaller fish (<900 mm TL). We sectioned otoliths for larger gag (>899 mm TL) to facilitate reading outer rings.

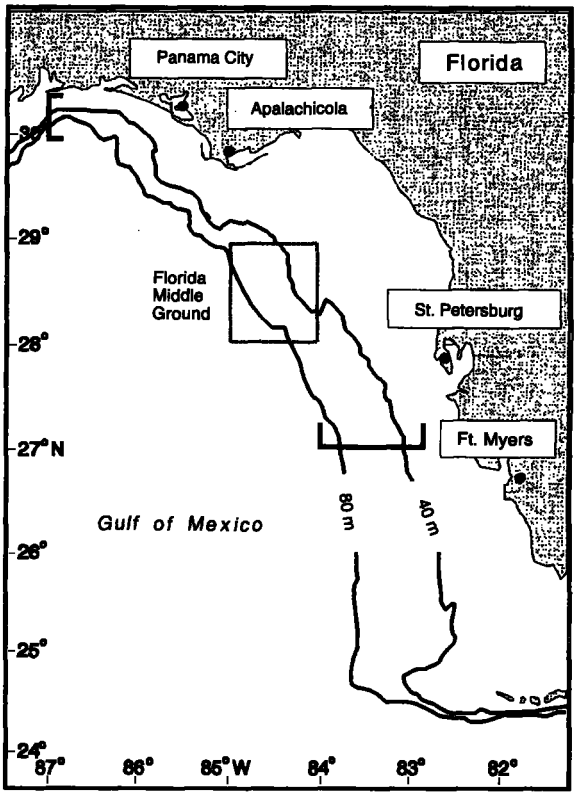

Figure 1

Area sampled for gag from commercial and recreational catches, 1991–94. Total area sampled, along the 40–80 m contour, is encompassed by brackets; most samples were collected from gag caught in the area south of Panama City to the Florida Middle Ground (the latter is indicated by the box).

Results

Of all the gag collected from February 1991 through December 1994 (n=2,046), most (61.7%) were taken from February through May between Panama City and the Florida Middle Ground (Fig. 1). A few samples were collected from off Pensacola, St. Petersburg, and Ft. Myers, FL. The majority of commercial and recreational landings were <24 h old when sampled. Depth data recorded with samples were predominately from commercial catches (57.2%). Commercial catches were usually from greater water depths (mean=57.2 m, n=697) than those for recreational catches (mean=32.6 m, n=73). Most 1991 samples (n=463) were from the commercial fishery (78.1%). Most 1992 samples (n=318) were from the recreational fishery (85.5%). Samples in 1993 (n=617) came from each of the fisheries in approximately equal numbers (commercial =49%). Most 1994 samples (n=648) were from the commercial fishery (68.6%).

Because neither oocyte diameter-frequency distributions for oocytes >0.08 mm in diameter (α=0.05; Kolmogorov-Smirnov two-sample test; $d_{0.05}$=0.1103;

Table 1

Effect of location of gag tissue samples on hydrated oocyte counts per unit of weight (g). Locations are anterior (1), mid (2), and posterior (3) of ovarian lobes. Analysis of variance indicates significance of location within a lobe for number of hydrated oocytes per gram of tissue. SS = sum of squares; MS = mean square.

Positions of sample in ovary	Lobe 1			Lobe 2			Both lobes		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
1	918	92	6	951	107	6	934	97	12
2	914	81	6	932	180	6	923	133	12
3	875	140	6	931	144	6	903	138	12
Total	902	103	18	938	138	18	920	121	(36)

Source	df	SS	MS	F	$P>F$
Lobe	1	11,460.23	11,460.23	0.74	0.40
Region	1	6018.21	6018.21	0.39	0.54
Interaction	1	803.81	803.81	0.05	0.82
Error	32	496,556.28	15,517.38		
Total	35	514,838.52			

n=5,450 oocytes; range=0.04 to 1.20 mm) nor hydrated oocyte counts per gram (Table 1) differed significantly among ovarian regions, we randomly sampled one region on each ovary to determine maturation stage, maximum oocyte diameter, and fecundity. Gag hydrated ovaries contained a mean of 920 hydrated oocytes per gram of ovarian tissue (range=875 to 951, SD=121, n=6 fish) (Table 1). The distinct clusters of oocytes of various diameters, including stage-1 and stage-2 oocytes, in gag ovaries throughout the spawning season indicated that gag is a multiple and indeterminate spawner.

Gag ovaries were usually much larger than testes (mean ovary weight=46.5 g, mean testes weight= 26.7 g). The largest ovary and testes weighed 1.60 kg and 120.0 g, respectively. Wormlike parasites were common in ovaries. Histological appearance of gag ovaries (nontransitional) was typical for marine teleosts (Wallace and Selman, 1981), except that some functional females appeared to contain crypts of spermatogonia.

An unusual condition observed in three females (stage 1 or 2) was the presence of a 5-mm thick lining (around the inside perimeter of the abdominal cavity) of compressed, hydrated oocytes apparently caused by rupture of the ovarian wall. These three fish were caught after the peak spawning season (May 1994, June 1993, and July 1994). We found no such lining in any of the other specimens examined.

We found that sex determinations and maturation-stage determinations were made with variable accuracy in fresh and histologically prepared samples. The two examinations gave the same results 89% of the time for sex determination but only 70% of the time for stage determination. The main reason for this poor comparison of the two staging techniques was that we could not accurately identify spent females (with POFs) or transitional males from fresh samples, because POFs and sperm could only be positively identified histologically.

Sex ratio

Sex ratio from all random samples (pooling data for 1991–93) was approximately 49 females: 1 male. Our emphasis on collecting gag with dark ventral pigmentation in 1994 clearly increased the overall percentage of males: 52.5% of all males for 1991–94 (n=59) were collected in 1994. Percentage of males was 1.9% in 1991–93 and 4.7% in 1994. Females were collected year round and males were collected in all months but January. Possible early transitional male gag (n=3) were found only during February, April, and May.

Ventral pigmentation

Gag with heavy ventral pigmentation (n=62) were collected in all months but January and March in waters >41 m (Table 2). Sex determination (n=60) showed that 5% were females (Fig. 2A), 3.3% were possible transitional males (Fig. 2, B and C), and 91.7% were males (Fig. 2D). Sex and stage were homogeneous among six gonad regions in all heavily pigmented fish.

Spawning period

Winter-spring spawning, indicated by the presence of hydrated oocytes, was corroborated by GSI (Fig.

Table 2

Results of histology on gonads of gag observed with heavy ventral pigmentation, 1991–94 (M = male, F = female, T = possible early transitional male). Stage (see "Methods" section): 1 = primary growth; 3 = vitellogenic; 4 = hydrated; 6 = possible sperm crypts; 7 = inactive; 8 = active; 9 = ripening; and 10 = ripe. C = commercial and R = recreational. Numbers in parentheses indicate number aged.

Year and month	*n*	Total length (mm)	Age (yr)	Gonad wt.(g)	Catch depth (m)	Fishery	Sex	Stage
1991								
Feb	1	985	—	31.2	—	C	T	6
	1	886	—	15.4	45.7–54.9	C	M	8
May	2	1140,1150	12,14	47.2,69.4	—	C	M	10
Sep	1	1140	—	33.1	—	R	M	10
Dec	1	1170	—	28.9	—	C	M	10
Total	6	886–1170	12,14 (2)	15.4–69.4	45.7–54.9	C,R	T,M	6–10
1992								
Jun	2	1100,1162	8,11	19.2,22.4	—	R	M	8–10
Oct	1	1276	20	8.9	39.6–[1]	R	M	9
Dec	6	965–1143	11 (1)	24.7–58.6	57.9–68.6	C	M	7–10
Total	9	965–1276	8–20	8.9–58.6	57.9–68.6	C,R	M	7–10
1993								
Feb	1	1170	17	84.5	54.9–76.2	C	M	10
	1	858	7	54.6	—	R	F	3
Jun	1	1030	9	55.2	—	R	F	1
Jul	6	1070–1290	10–20	12.8–25.7	57.9–59.4	C,R	M	7–10
Aug	1	1105	11	13.9	54.9–67.1	C	M	9
Oct	2	1065,1095	13,–	13.6,17.9	115.8	C	M	9
Total	12	858–1290	7–20	12.8–84.5	54.9–115.8	C,R	M,F,T	1–10
1994								
Apr	8	980–1201	7–12	35.7–49.9	67.1–109.7	C	M	10
	1	1120	12	267.7	67.1	C	T	6
	1	1090	9	152.6	67.1	C	F	4
May	11	1055–1240	8–22	6.4–120.0	53.3–106.7	C	M	8–10
Jul	4	1130–1210	11–20	12.8–22.7	54.9–99.1	C	M	9–10
Aug	4	1085–1235	—	18.2–27.8	79.2	C	M	9–10
Sep	1	1175	—	40.9	50.3	C	M	10
Oct	1	1242	—	30.9	79.2	R	M	10
Nov	1	1230	—	21.8	—	C	M	10
Dec	1	981	—	5.4	41.1-44.2	C	M	10
Total	33	980–1240	7–22	5.4–267.7	41.1–109.7	C	M,F,T	4–10
Grand total (1991–94)	60	858–1290	7–22	5.4–267.7	41.1–115.8	C,R	M,F,T	1–10

[1] Questionable depth from spearfishing tournament.

3, A and B). Female GSIs (n=1,695) ranged from 0.01 to 8.29, with greatest mean GSI (0.21–2.60) occurring from February through March in all years (Fig. 3A). Male GSIs (n=59) ranged from 0.02 to 0.82, with greatest GSI occurring during February (n=1) in 1991 (Fig. 3B). Possible early transitional male GSI (n=1) was 1.65 in April 1994 (only one possible transitional male with an intact gonad and an accurate total weight was collected).

Histological staging of ovaries collected in 1993 (n=209) and 1994 (n=437) also confirmed winter–spring spawning (Fig. 4). All ovaries were stage 1 from June through September and stage 2 from October through January. Stage-3 ovaries first appeared in December and stage-4 in February. Stage-4 and stage-5 ovaries indicated that spawning occurred from February through April in 1993–94, corroborating GSI analysis. Stage-5 ovaries (containing nondegenerating POFs) were extremely rare (n=7), occurring only in January, March, and July 1993, and April 1994. Small numbers of hydrated oocytes appeared as remnants in the center of stage-1 ovaries after the spawning season.

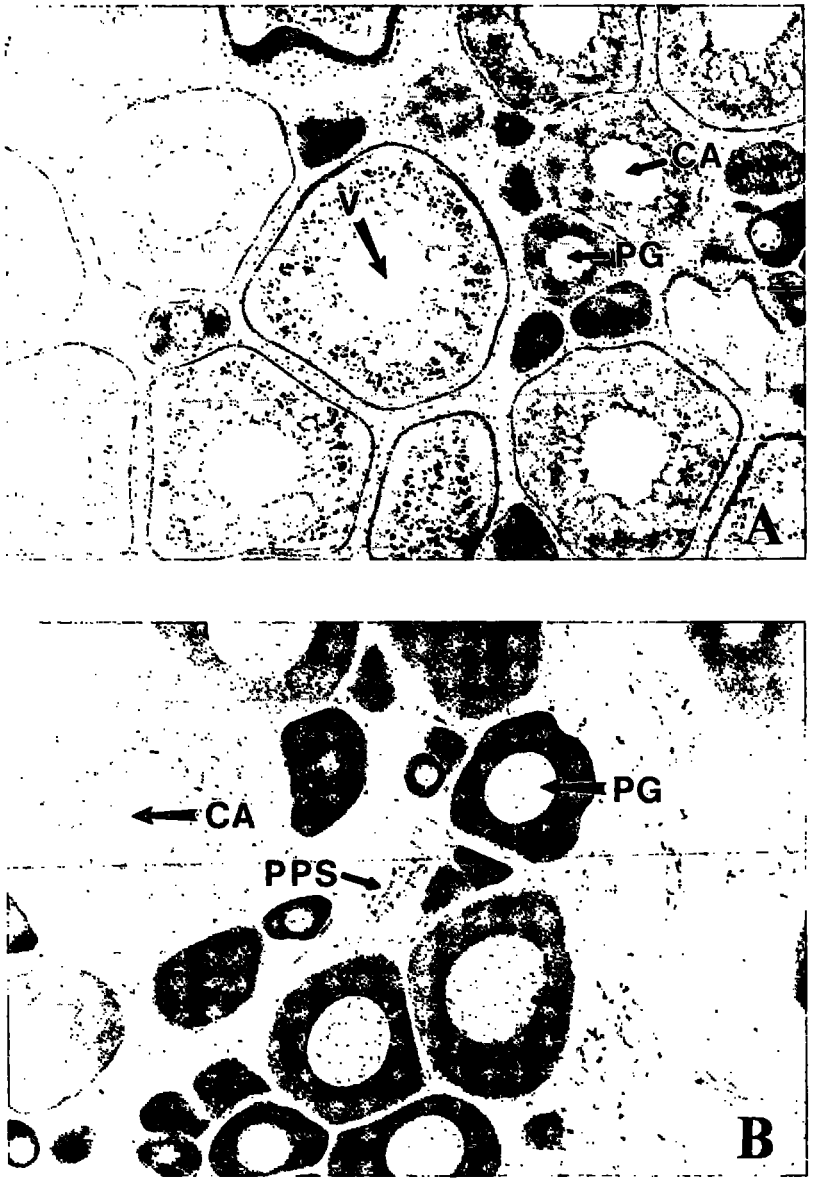

Figure 2

Photomicrographs of histological sections of gag with heavy ventral pigmentation: (**A**) ovarian tissue from an 858-mm-TL female caught in February 1993; (**B**) tissue from a 985-mm-TL possible early transitional male caught in February 1991; (**C**) tissue from a 1120-mm-TL possible early transitional male caught in April 1994; (**D**) testicular tissue with remnant oocytes from a 1143-mm-TL male caught in December 1992; PG = primary growth oocyte; CA = cortical alveolar oocyte; V = early vitellogenic oocyte, EHO = early hydrated oocyte (with coalescing yolk globules); PPS = possible primary spermatocytes; PS = primary spermatocytes; SS = secondary spermatocytes; MS = mature spermatids; and RO = remnant oocyte. Magnification was 132× for A and 264× for B–D.

Spawning mainly occurred from February through April 1991–94, but some evidence of spawning also occurred in December, January, May, June, and July. A total of 173 stage-4 and stage-5 ovaries were found during February, March, and April (n=895). No hydrated ovaries and only one ovary with POFs were found during December (n=58) and during January (n=77). Only one hydrated ovary, one ovary with hy-

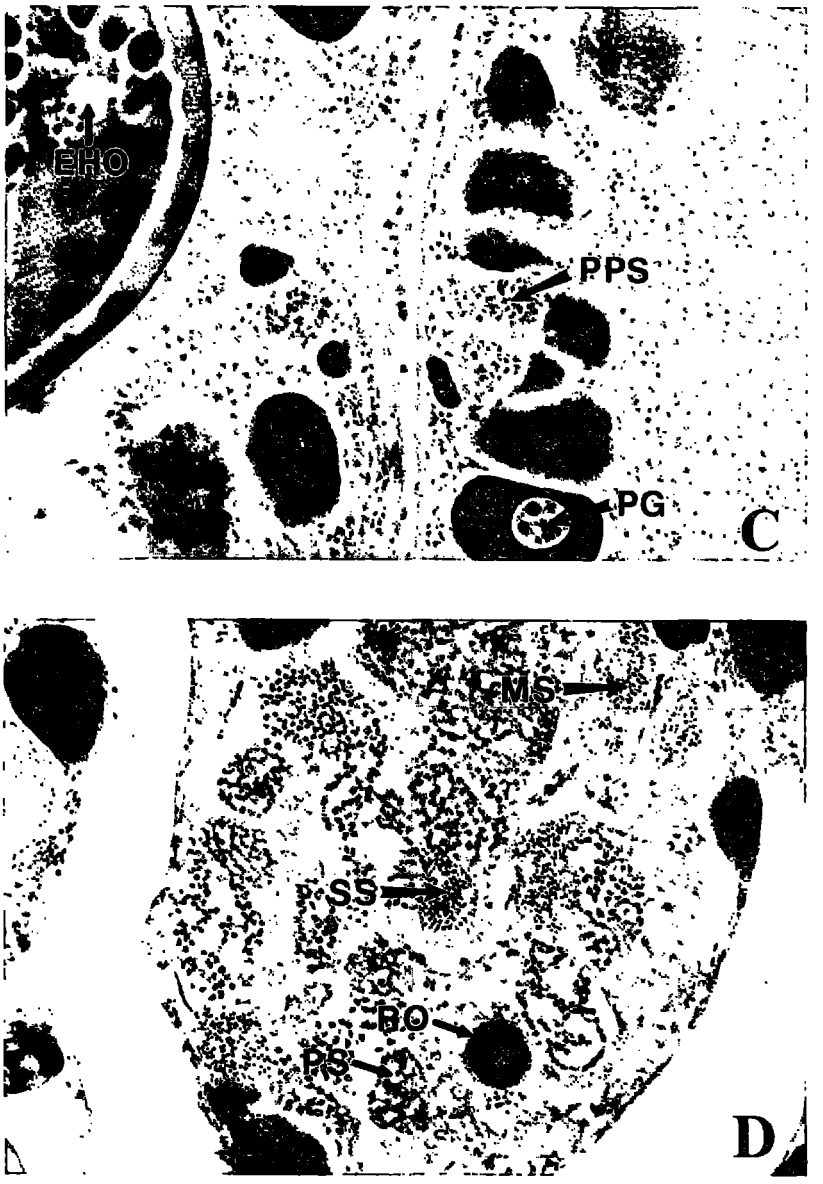

Figure 2 (continued)

drated oocyte remnants, and no ovaries with POFs were found during May (n=306). Hydrated oocyte remnants (in two ovaries) and POFs (in one ovary) were found in June (n=180) and July (n=159).

Length and age at first spawning, and depth of spawning

Length at first spawning (see "Methods" section for definition) was 710 mm TL in 1991, 570 mm TL in 1993, and 670 mm TL in 1994 for females, and 980 mm TL for males in 1994. Age at first spawning was 3 years for females and 7 years for males. Stage-4 females were caught at depths of 30 m and greater. All males were caught at depths greater than 41 m.

Batch fecundity

Batch fecundity estimates (n=39) ranged from 10,864 to 865,295 hydrated oocytes (Fig. 5). These estimates came from gag 690–1065 mm TL, 4.5–16.5 kg TW, 23.4–871.9 g ovary weight, and 3–9 years of age.

Regression analysis showed significant positive linear correlations between batch fecundity estimates

(BFE) and TL, gutted body weight (GBW), and age. Total length was the best predictor of batch fecundity (Fig. 5; $BFE = 1.773 \times 10^3(TL) - 1.119 \times 10^6$; r^2=0.600, P<0.0001, n=39); followed by GBW ($BFE = 5.942 \times 10^4(GBW) - 9.517 \times 10^4$; r^2=0.576, P<0.0001, n=35); then age ($BFE = 9.476 \times 10^4(\text{age}) - 1.213 \times 10^5$; r^2=0.474, P<0.0001, n=38).

Spawning frequency: by year, and age × year

Spawning frequency estimates were determined for females >709 mm TL in 1991, >576 mm TL in 1993, and >669 mm TL in 1994. Variations in spawning frequency were significantly different among years tested (t-test, P<0.02). Spawning frequency for females in 1991 was 27 times, with 29.3% (93/317) of individual females spawning at an average of every 3.4 d. Spawning frequency was not determined in 1992 owing to the absence of samples from January and February. Spawning frequency in 1993 was 14 with 16.1% (36/224) of individual females spawning at an average of every 6.2 d. Spawning frequency for 1994 was 8 with 14.0% (18/129) of individual females spawning at an average of every 7.2 d.

Spawning frequency also varied significantly among ages (t-test, P<0.01) and by age × year (ANOVA, P<0.05) for gag (n >5 per age × year) (Table 3; Fig. 6). Age-2 females in 1993 had a spawning frequency = 0, although one spawning female of this age occurred in 1994. Age-3 females in 1991 also had a spawning frequency = 0; 1993 and 1994 spawning frequencies were also low (6 and 7, respectively). Spawning frequency varied the most (6–71) among years for 4- to 8-yr-old gag. Nine year old gag spawned 41 times in 1991. All sample sizes for 10- to 12-yr-old, 16-yr-old, and 26-yr-old gag were inadequate (n<6) for estimation of spawning frequency.

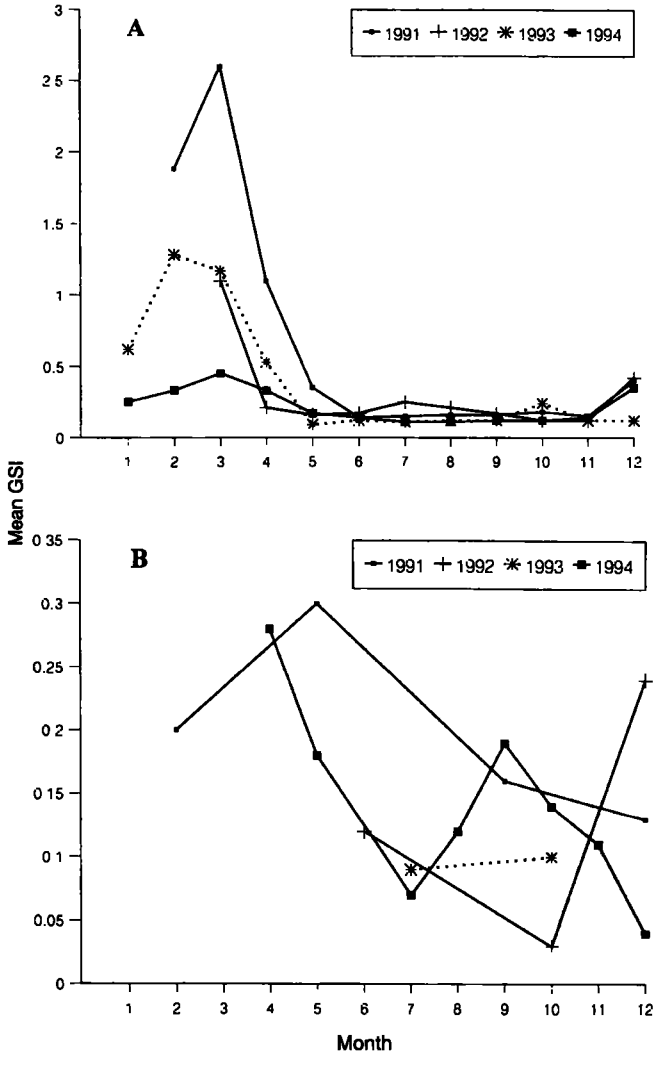

Figure 3

Mean gonadosomatic index (GSI) by month and year for gag. (**A**) females (n=1685) and (**B**) males (n=39) from the northeastern Gulf of Mexico, 1991–94. Note different scales for y axis in A and B.

Annual fecundity

Annual fecundity estimated with spawning frequency estimates by age and year ranged from 0.065 to 61.4 million (Table 4; Fig. 7). Only spawning frequencies for aged fish (n>5 per age and year) were used. Age was an effective predictor of annual fecundity (AFE=9.276 × $10^3(age)^{3.94}$; r^2=0.76, P<0.0001; n=33).

Discussion

We found both the peak and maximum length of the spawning period for gag to be slightly longer than previously determined (e.g. McErlean, 1963; Hood and Schlieder, 1992; Coleman et al., 1996; Koenig et al., 1996) in the Gulf of Mexico. Both GSI and percent frequency of hydrated oocytes and POFs were greatest in February through April, but a few POFs were present in December–January and May–July. Our sampling may not have included peak spawning from 1992 through 1994, as it had in 1991. McErlean (1963), through macroscopic examination of gonads, estimated that spawning occurred January through March. Hood and Schlieder (1992), through histological examination, showed that peak spawning occurred in

February and March and females were spent from December to May. Coleman et al. (1996) and Koenig et al. (1996) used GSIs, fresh "squashes," histological examinations, and juvenile otolith daily increments and found peak spawning to occur in February–March, but some gag were reproductively active from January through mid-May in 1991.

McErlean's (1963) estimates of (annual) fecundity in 7–8 yr-old gag (n=3, 930–946 mm TL) were somewhat similar to our batch fecundity estimates for the same age fish (his and our range of estimates were 0.526–1.457 million and 0.249–0.865 million, respectively) although the exact oocyte size and stage counted by McErlean are unknown. We can infer, however, from the "bright-yellow eggs" he counted (McErlean[3]) that they were vitellogenic (nonhydrated) oocytes because fresh hydrated oocytes are clear. We counted only hydrated oocytes (n=12 fish, 860–1065 mm TL). McErlean's ovary weights averaged 231.1 g, whereas ours averaged 656.7 g. This comparison of ovary weight of similar size and age fish strongly suggests that McErlean's gag were not ready to spawn. Gag population changes between 1961 (McErlean, 1963) and 1991–94 (present study) may also have affected length, age, ovary weight, and fecundity (Johnson et al., 1993).

Our estimates of gag batch fecundity (0.011–0.865 million), spawning frequency by age and year (6–71; see Tables 3 and 4), and annual fecundity (0.065–61.4 million) are similar to those of several multiple spawning, demersal marine species similar to gag in size and longevity. Fitzhugh et al. (1993) estimated mean batch fecundity (1.6 million) and spawning frequency (46, n=25) for black drum, *Pogonias cromis*, whereas Nieland and Wilson (1993) estimated ranges of batch fecundity (0.510–2.42 million), spawning frequency (25–28), and annual fecundity (13.0–67.0 million, n=41) for the same species. Wilson and Nieland (1994) estimated batch fecundity (0.160–3.27 million), and their data indicated a spawning frequency of 1–30 (calculated by the senior author (LAC) of this paper) for red drum, *Sciaenops ocellatus* (n=51). Recently, Collins et al. (1996) estimated batch fecundity (0.001–1.70 million), spawning frequency (21–35), and annual fecundity (0.012–59.7 million) for red snapper, *Lutjanus campechanus* (n=66).

Spawning frequencies and possibly GSIs may be useful in forecasting trends in fishery production. For instance, our estimates of GSI and spawning frequency were greatest during 1991 and 1993, suggesting that population reproductive efforts may have been greater and gag juveniles may have been more

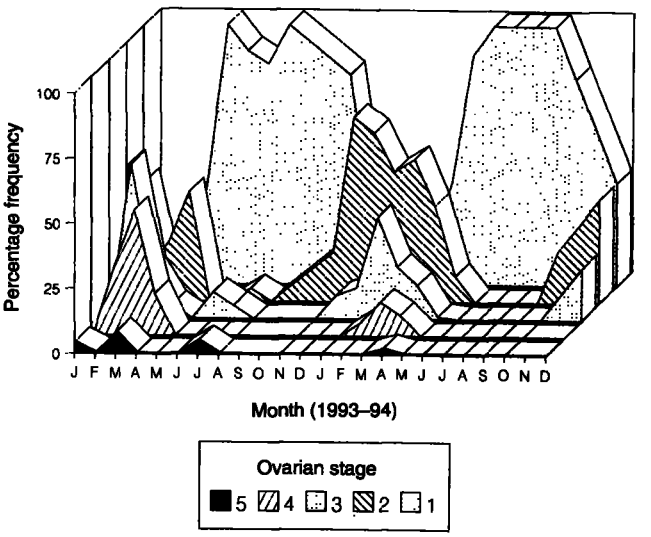

Figure 4

Percentage frequency of gag ovarian stages examined histologically by month and year, 1993–94 (n=636).

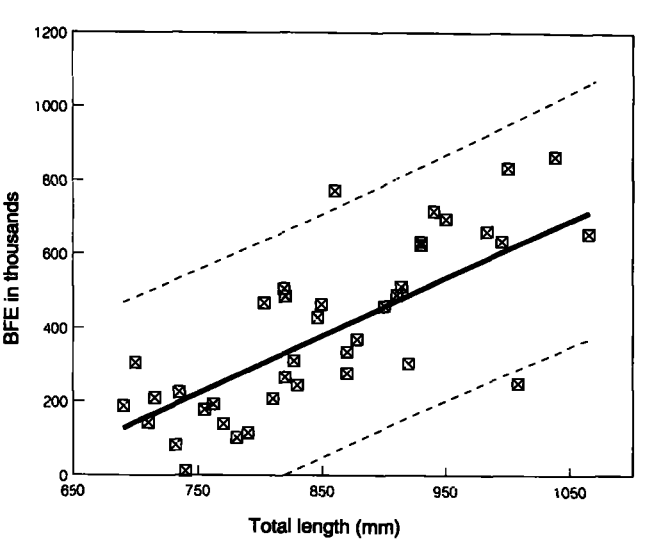

Figure 5

Gag batch fecundity estimates (BFE) plotted and regressed against total length (TL): $BFE = 1.773 \times 10^3 (TL) - 1.119 \times 10^6$ (r^2=0.60, P<0.0001, n=39), and 95% confidence limits (lighter line above and below bold regression line).

[3] McErlean, A. J. [retired]. 1997. 4364 Hickory Shores Blvd., Gulf Breeze, FL 32561. Personal commun.

abundant in these years. This finding is corroborated by studies of Johnson and Koenig (in press), wherein abundance of age-0 gag in north Florida seagrass beds was higher in 1991 and 1993 than it was in 1992 and 1994. Johnson and Koenig (in press) also found that an alternating pattern of abundance was evident in the age structure of the gag fishery from 1984 through 1989, with odd years producing dominant year classes, if the same number of females are assumed to spawn each year.

Table 3

Spawning frequency estimates (SFEs) by age and year for female gag (≥total length (TL) of smallest female with hydrated oocytes (HOs) or postovulatory follicles (POFs) during the spawning season).

Age (yr)	Year	*n*	*n* with HOs/POFs	% with HOs/POFs	SFE
2	91	0	—	—	—
	93	6	0	0	0
	94	1	1	100.0	57
3	91	9	0	0	0
	93	119	8	6.7	6
	94	8	1	12.5	7
4	91	20	6	30.0	28
	93	10	2	20.0	17
	94	78	8	10.3	6
5	91	105	28	26.7	25
	93	34	6	17.6	15
	94	8	1	12.5	7
6	91	8	2	25.0	23
	93	13	4	30.8	26
	94	12	3	25.0	14
7	91	13	1	7.7	7
	93	28	13	46.4	40
	94	2	0	0	0
8	91	6	1	16.7	16
	93	6	5	83.3	71
	94	8	2	25.0	14
9	91	9	4	44.4	41
	93	1	1	100.0	85
	94	2	0	0	0
10–12	91	2	1	50.0	47
	93	0	—	—	—
	94	3	1	33.0	19
16	91	1	0	0	0
	93	0	—	—	—
	94	0	—	—	—
26	91	1	0	0	0
	93	0	—	—	—
	94	0	—	—	—
3–26	91	174	43	24.7	23
2–9	93	217	39	18.0	15
2–12	94	122	17	13.9	8

The scarcity of nondegenerating POFs and the relatively low r^2 values of regression equations suggest that some of our annual fecundity estimates are low, a problem prevalent in some past studies on other species (Nieland and Wilson, 1993; Taylor and Murphy, 1992). The age of POFs is an important factor in judging whether POFs in a sample are from the same spawn as that for hydrated oocytes (Fitzhugh and Hettler, 1995). Delayed preservation in formalin may have caused some incompletely spawned ovaries to appear fully hydrated (if the fragile POFs were lost [Hunter et al., 1985], thus causing low estimates of batch fecundity, spawning fre-

Table 4

Data used for gag annual fecundity estimation, 1991–94. SFE=spawning frequency estimate by age and year.

Catch date	Total length (mm)	Age (yr)	Batch fecundity estimate	SFE	Annual fecundity estimate
1991					
21 Mar	820	5	265,294	25	6,632,350
5 Apr	732	4	82,183	28	2,301,124
5 Apr	755	5	176,552	25	4,413,800
5 Apr	810	5	208,438	25	5,210,950
8 Apr	830	5	243,231	25	6,080,775
8 Apr	870	5	276,416	25	6,910,400
8 Apr	710	5	144,265	25	3,606,625
1993					
25 Feb	870	7	335,275	40	13,411,000
25 Feb	1065	7	657,268	40	26,290,720
25 Feb	1038	8	865,295	71	61,435,945
25 Feb	950	8	696,251	71	49,433,821
20 Mar	860	7	772,158	40	30,886,320
21 Mar	878	8	368,974	71	26,197,154
21 Mar	914	8	510,637	71	36,255,227
22 Mar	983	7	661,993	40	26,479,720
23 Mar	1000	8	834,425	71	59,244,175
23 Mar	930	6	625,159	26	16,254,134
28 Mar	762	3	191,767	6	1,150,602
29 Mar	920	5	302,604	15	4,539,060
29 Mar	715	3	208,878	6	1,253,268
29 Mar	740	3	10,864	6	65,184
29 Mar	820	5	484,514	15	7,267,710
29 Mar	900	5	458,392	15	6,875,880
29 Mar	930	6	633,481	26	16,470,506
29 Mar	995	7	635,329	40	25,413,160
29 Mar	940	7	717,445	40	28,697,800
3 Apr	700	3	304,997	6	1,829,982
3 Apr	735	3	224,684	6	1,348,104
1994					
15 Mar	846	4	428,371	6	2,570,226
15 Mar	690	4	187,216	6	1,123,296
15 Mar	827	5	310,357	7	2,172,499
15 Mar	910	6	487,719	14	6,828,066
6 Apr	1008	8	249,162	14	3,488,268

quency, and annual fecundity). Varying amounts of "missing" hydrated oocytes due to partial spawning would have then caused the low r^2s. An incomplete hydration process in some of the gag is another possible explanation for the low r^2 values; samples were taken from gag caught at different times of the day, causing variable hydration (Hunter et al., 1985). Relatively low r^2 values for the relation between batch fecundity and length and weight were also found for black drum (r^2<0.47, in Nieland and Wilson, 1993) and swordfish, *Ziphias gladius* (r^2<0.41, in Taylor and Murphy, 1992). Because dockside sampling was also used in these studies, delayed preservation may have caused some black drum and swordfish POFs to be missed, thereby causing low r^2 values.

In this study, we used histological sections to identify sex in gag with heavy abdominal pigmentation. Because male behaviors are associated with fish demonstrating this pigment pattern (Gilmore and Jones, 1992), the assumption is widespread that all these fish are males. Yet we found that 5% of such pigmented fish were females. It is possible that these fish were actually in the early stages of sex change, a phase undetectable even with histology.

Our observation of a lining of hydrated oocytes around the outside of the abdominal cavity in gag suggests that the ovary or the oviduct, or both, had ruptured at the time of hydration. This rupture probably did not occur during the fish's capture and handling because the lining of hydrated oocytes was dry and firm when we observed this phenomenon on the boat. A similar rupture may have occurred in a captive population of laboratory-matured female gag where two individuals spontaneously developed hydrated oocytes but did not ovulate; no oocytes were shed although no ovarian rupture was noted, possibly due to the absence of a male.[4] Although the proportion of males required for adequate fertilization is unknown for gag, the sharp decline of males observed by Coleman et al. (1996), Koenig et al. (1996), McGovern et al. (in press), and in this study suggests a restricted availability of males during the spawning period. Ovarian hydration in females in the absence of males could lead to ovarian rupture.

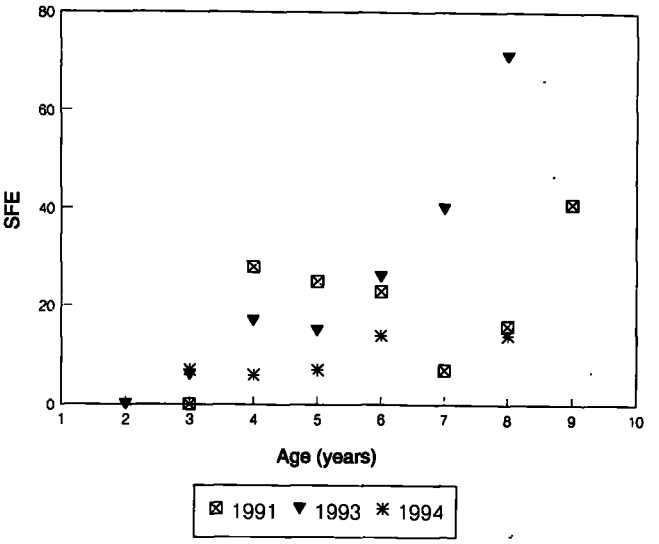

Figure 6

Gag spawning frequency estimates (SFE) by age and year, for ages with n>5 by year.

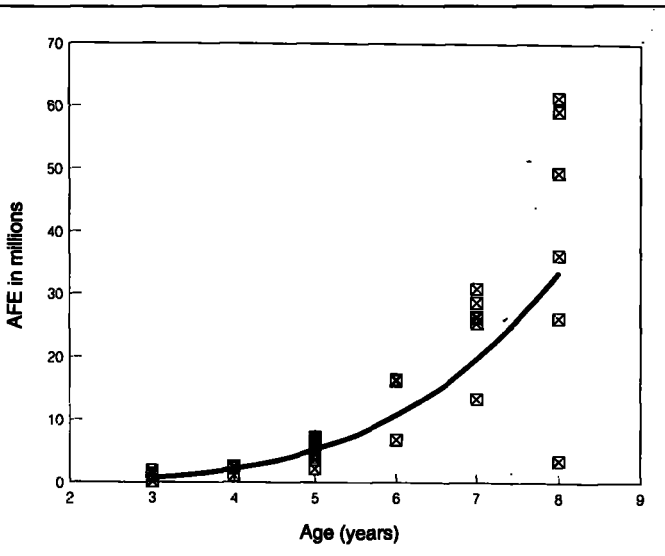

Figure 7

Gag annual fecundity estimates (AFE) plotted and regressed against age in years: $AFE = 9.280 \times 10^3 (age^{3.94})$ (r^2=0.76, P<0.0001, n=33).

Although recent studies have increased our knowledge of gag reproduction, several significant questions remain. Gag appear to spawn at a discrete depth; therefore should only those females from a known spawning area be used for spawning frequency and fecundity estimates? Do fewer males in proportion to females prevent some mature female gag from spawning every year (Coleman et al., 1996;

[4] Carr, W. 1992. Whitney Laboratory, University of Florida, St. Augustine, FL. Personal commun.

Koenig et al., 1996)? Would oocytes hydrate and then be resorbed if there was no male in close proximity? Can gag spawn as females early in the spawning season, change sex, and then spawn as males late in the same season, as suggested for red grouper, *Epinephelus morio*, by Moe (1969)? Would measurement of hormones be a better indicator of the state of transition than our histological examination? Does the possibility that sex change in serranids may occur quickly (captive *Anthias squamipinnis* changed from female to male in two weeks [Fishelson, 1970]) explain why our number of possible early transitional males was low? Questions such as these can only be answered with specifically designed laboratory and field studies.

Acknowledgments

We are indebted to many persons and organizations. Several commercial fishermen in the Panama City, Florida, area allowed us to sample their catches, including Captains Ray Ward, Sigurd Smeby, Mark Raffield, Mike Raffield, Dannie Lee, and Steve Smeby. Jerry and Carl Anderson let us routinely sample their seafood markets at Panama City Beach. Charterboat captains Bill Archer and Charles Paprocki also participated in sampling. Special thanks are extended to NMFS Fishery Reporting Specialist Debbie Fable for her help in the field. Bruce Thompson, Jeff Render (deceased), and Cheryl Crowder (Louisiana State University) advised us on methods and ovarian histology. Lewis Bullock, Ron Taylor, and Ruth Reece (Florida Marine Research Institute, St. Petersburg) effectively helped with sampling, methods, and histology. David Wyanski (South Carolina Dep. Natural Resources, Charleston) assisted with identification of transitional males. Reviews by Felicia Coleman, Gary Fitzhugh, Yvonne Sadovy, and Lewis Bullock greatly improved the manuscript. Technical support was provided by Andrew David, John Brusher, Chris Keim, Marc Remy, Sean Murray, Mike Strohmenger, John Dahl, Sandra Neidetcher, Guy Pizzuti, and Sara Heath (NMFS, Panama City). Carol Parker and Betsy Black typed many drafts of this ms. This research was funded by the MARFIN (Marine Fisheries Initiative) Program of the NMFS, Southeast Region (Grant #94 MFIH09).

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