Reproductive biology of cobia, *Rachycentron canadum*, from coastal waters of the southern United States

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Abstract—Reproductive biology of the cobia, *Rachycentron canadum*, is described from four coastal areas in the southern United States. Samples were obtained from recreational fishermen between December 1995 and November 1997 from the southeastern United States (Morehead City, NC, to Cape Canaveral, FL), the eastern Gulf of Mexico (Ft. Myers to Crystal River, FL), the north-central Gulf of Mexico (Destin, FL, to Chandeleur Islands, LA) and the western Gulf of Mexico (Port Aransas, TX). Histological evidence of spawning occurred from April through September in all areas. Some female cobia (17–32%) throughout the Gulf of Mexico had spent or regressed ovaries by July. Gonadosomatic index peaked between May and July throughout the region. Ovaries of females from all areas contained both postovulatory follicles (POF) and oocytes in final oocyte maturation (FOM) during all months of the reproductive season. Batch fecundity was calculated by using three different methods: oocytes >700 µm were fixed in 1) Gilson's fixative or 2) 10% neutral buffered formalin (NBF), and 3) oocytes undergoing FOM were sectioned for histological examination. Mean batch fecundity ranged from 377,000 ±64,500 to 1,980,500 ±1,598,500 eggs; there was no significant difference among methods. Batch fecundity calculated with the NBF method showed a positive relationship with fork length (P=0.021, r^2=0.132) and ovary-free body weight (OFBW; P=0.016, r^2=0.143). Relative batch fecundity was not significantly different among months during the spawning season and averaged 53.1 ±9.4 eggs/g OFBW for the NBF method and 29.1 ±4.8 eggs/g OFBW for the FOM method. Although spawning frequencies were not significantly different among areas (P=0.07), cobia from the southeastern United States and north-central Gulf of Mexico were estimated to spawn once every 5 days, whereas cobia from the western Gulf of Mexico were estimated to spawn once every 9 to 12 days.

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Fish. Bull. 99:15–28 (2001).

The cobia, *Rachycentron canadum* (Goode, 1884), is a large coastal pelagic fish found worldwide in tropical and subtropical waters with the exception of the eastern Pacific (Shaffer and Nakamura, 1989). The cobia is a highly prized recreational species and record size fish have been caught in coastal waters off the southern United States, as well as off Western Australia, Nigeria, and Kenya (International Game Fish Association, 1998). Most specimens captured in the southern United States are landed by recreational anglers along the southeastern U.S. coast and in the Gulf of Mexico; however, some are caught incidentally by U.S. commercial fisheries, particularly in Florida waters (Shaffer and Nakamura, 1989).

Cobia are specifically targeted by a growing number of anglers in the southern United States, as evidenced by the increase in fishing tournaments for cobia. Information on age, growth, and seasonal movement is being collected through tagging programs in Virginia, Florida, Mississippi, and Louisiana (International Game Fish Association, 1998), and the age and growth of cobia from the north-central Gulf of Mexico was recently described by Franks et al. (1999). Limited information on the reproductive biology of cobia from the southern United States includes descriptions of the eggs, larvae, and juveniles from Chesapeake Bay (Joseph et al., 1964), North Carolina (Hassler and Rainville, 1975), and the northern Gulf of Mexico (Ditty and Shaw, 1992). Summer spawning of cobia has been reported from Chesapeake Bay (Richards, 1967), North Carolina (Smith, 1995), the northern Gulf of Mexico (Dawson, 1971; Burns et al.[1]), Louisiana (Thomp-

[1] Burns, K. M., C. Neidig, J. Lotz, and R. Overstreet. 1998. Cobia (*Rachycentron canadum*) stock assessment study in the Gulf of Mexico and in the South Atlantic. Final Rep., MARFIN Coop. Agreement NA57FF0294 to NMFS (NOAA), 108 p. Mote Marine Laboratory, 1600 Thompson Parkway, Sarasota, FL 34236.

son et al.[2]) and Texas (Finucane et al.[3]). Biesiot et al. (1994) described the biochemical changes in developing ovaries of cobia from the northern Gulf of Mexico and reported that spawning occurred during spring and summer. The most comprehensive information on cobia reproduction to date provides a detailed description of the gonadal maturation and spawning season for cobia from the north-central Gulf of Mexico (Lotz et al., 1996) and furnishes evidence that cobia are multiple, or batch spawners. Lotz et al. (1996) estimated batch fecundity on the basis of the largest mode of oocytes, but they did not estimate spawning frequency.

Our study was undertaken to document more thoroughly the reproductive biology of cobia from the southern region of the United States. Specifically, we describe and compare the spawning seasons and gonadal development from four coastal areas: the southeastern United States, the eastern Gulf of Mexico, the north-central Gulf of Mexico, and the western Gulf of Mexico. Additionally, batch fecundity and spawning frequency are estimated for cobia from the region. The results are discussed in light of the migratory nature of cobia throughout coastal waters of the southern United States.

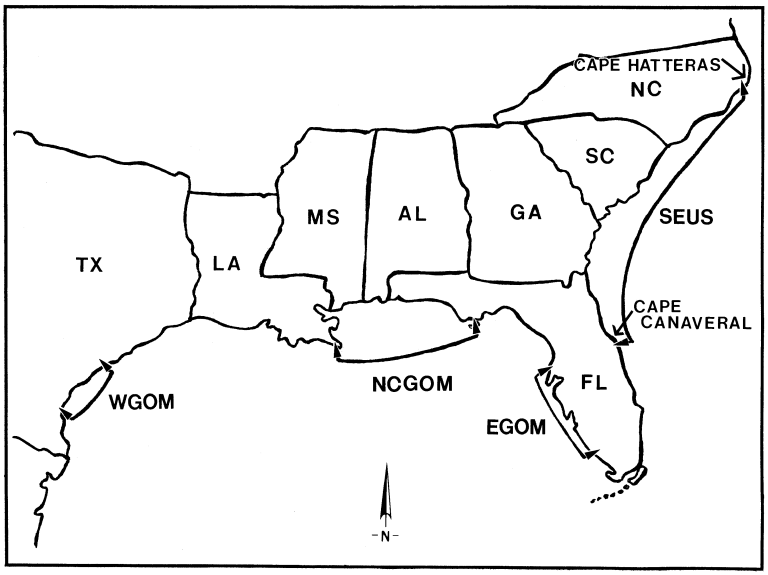

Figure 1

Areas sampled for cobia within the southern United States. SEUS = southeastern United States; EGOM = eastern Gulf of Mexico; NCGOM = northcentral Gulf of Mexico; WGOM = western Gulf of Mexico.

Materials and methods

Sample collection

Cobia were sampled from the coastal waters of four general regions in the southern United States (Fig. 1). The regions were defined as the southeastern United States (SEUS; Morehead City, North Carolina, to Cape Canaveral, Florida), the eastern Gulf of Mexico (EGOM; Ft. Myers to Crystal River, Florida), the north-central Gulf of Mexico (NCGOM; Destin, Florida to the Chandeleur Islands, Louisiana), and the western Gulf of Mexico (WGOM; Port Aransas area, Texas). In our study, coastal waters are defined as those extending over the continental shelf for 20 km in the Atlantic Ocean and for 80 km in the Gulf of Mexico.

We sampled cobia opportunistically from the recreational and charter boat fisheries from December 1995 to December 1997. Additional samples were taken in the north-central Gulf of Mexico during February and March 1999. Sampling teams were present at major cobia fishing tournaments throughout the study area; most samples from the SEUS and the NCGOM came from fishing tournaments. The majority of the cobia sampled from the EGOM were captured by nontournament recreational anglers. All fish from Texas were obtained from one charter boat captain during regular fishing trips. Anglers were interviewed to determine the location of capture of each fish. Fork length (FL, cm) and total weight (TW, g) were recorded at the dock and gonads were excised and placed on ice for transport to the laboratory. In the laboratory, gonads were weighed to the nearest 0.1 g (gonadal weight [GW]) and the gonadosomatic index (GSI) was calculated by using the formula

$$GSI = [GW/(TW - GW) \times 100].$$

Fish weights were unavailable from the WGOM; hence GSIs were not calculated for this region. Sections were removed from both left and right gonads and preserved in 10% neutral buffered formalin (NBF) for histological analysis. Cobia have been shown previously to have homogeneous oocyte development within the ovary (Lotz et al., 1996); thus, multiple sections of the same ovary were not removed for analysis. For fecundity analysis, two portions (approximately 5 g each) of the ovary were removed, weighed to the nearest 0.1 g, and preserved in Gilson's fixative (GF) and 10% NBF, respectively.

Histological analysis

Tissues were placed into individually labeled cassettes and rinsed with running tap water overnight prior to de-

[2] Thompson, B. A., C. A. Wilson, J. H. Render, M. Beasley, and C. Cauthron. 1992. Age, growth and reproductive biology of greater amberjack and cobia from Louisiana waters. Final Rep., MARFIN Coop. Agreement NA90AA-H-MF722 to NMFS (NOAA), 77 p. Coastal Fisheries Institute, LSU Center for Coastal, Energy and Environmental Resources, Baton Rouge, LA 70803.

[3] Finucane, J. H., L. A. Collins and L. E. Barger. 1978. Ichthyoplankton/mackerel eggs and larvae. Environmental studies of the south Texas outer continental shelf, 1977. Final rep. to Bur. Land Manage. Natl. Mar. Fish. Serv., NOAA, Galveston, TX 77550.

hydration and embedment in paraffin, following standard histological techniques. The paraffin blocks were sectioned at 4 µm by using a rotary microtome. Duplicate slides were prepared for each tissue, resulting in a total of four slides for each cobia specimen (two from each gonad). The slides were stained with Gill's I hematoxylin and eosin phloxine (Polyscientific Corporation) following standard histological procedures.

Three separate views from each side of the gonad of each fish were examined to determine maturity stages. Ovarian maturity classes were based on those previously described for cobia by Lotz et al. (1996). The entire ovarian section was examined for the presence of postovulatory follicles (POF) and oocytes undergoing final oocyte maturation (FOM). POF stages were classified following the methods of Hunter et al. (1986), although age estimates for POF stages in cobia are unverified. FOM stages were classified following Brown-Peterson et al. (1988). Following inspection of the entire ovarian section, three areas were arbitrarily selected from each slide for quantification of oocytes. Oocytes in all stages of development (including atretic oocytes) and POFs were counted at 100× and the percentage of each oocyte stage in the field of view was estimated. Oocyte atresia stages were classified by following the methods of Hunter and Macewicz (1985a).

The entire testicular section from each cobia was examined to determine the maturity classification for male fish. Three arbitrarily selected portions of each section were examined at 100× and 400× to classify all stages of spermatogenesis observed. Testicular maturity stages were based on those described for cobia by Lotz et al. (1996). Particular attention was given to the presence and amount of spermatogenesis in the testis.

Estimates of batch fecundity

Batch fecundity was estimated from the counts of oocytes in samples of ovarian tissue. Oocyte counts were obtained after teasing oocytes from tissues fixed in either GF or NBF for three to four months or from histological evaluation of tissue sections. The volumetric method was used to estimate fecundity for tissues fixed in GF or NBF (Bagenal and Braum, 1971). All oocytes freed from each GF or NBF sample were placed in 50 mL of water, stirred to homogeneity, and ten 1-mL samples were removed, combined, and the total volume brought to 50–70 mL with water. The diluted sample was stirred to homogeneity and 1-mL subsamples were removed, counted and replaced three to six times for each ovarian sample. All oocytes >700 µm from each subsample were counted and measured by using a stereo dissecting microscope and a computerized image analysis system. Oocytes of this size were used because Lotz et al. (1996) previously showed that cobia have a distinct mode of large oocytes prior to spawning. Typically, 25–100 oocytes were measured and counted in each subsample.

Estimates of batch fecundity based on histological evaluation were obtained by counting the number of oocytes undergoing FOM in six fields under a compound microscope at 100× magnification. The area of a single field of view was determined to be 0.0249 cm^2 by using a stage micrometer. The number of oocytes in final maturation observed in a field of view was converted to the number per mL by the formula

$$N \times 0.0249^{3/2} = N \times 0.003939.$$

FOMs were counted as 1 if ≥50% of the oocyte was in the field of view and were uncounted if <50% of the oocyte was in the field of view. The total number of FOMs in a fish was then determined by multiplying the estimated number per mL by the total volume of the ovaries. In all cases, fecundity was expressed as both batch fecundity (mean number of eggs/batch) and relative fecundity (number of eggs/gram of ovary-free body weight).

Ovarian volume was determined by volumetric displacement. The observed relationship between ovarian weight and ovarian volume was determined and that relationship was used to estimate ovarian volumes of fish for which direct volume measurements were unavailable. The analysis was restricted to fish with ovarian weights >500g.

Estimates of spawning frequency

Two methods based on histological observations were used to estimate spawning frequency of cobia: 1) the percentage of females in the late developing ovarian class with 0- to 24-h POF in the ovary and 2) the percentage of females in the late developing ovarian class undergoing FOM. Only fish in the late developing ovarian class were included in these analyses, because this is the only class in which cobia have the potential to spawn. For both methods, estimates of spawning frequency were determined according to the procedure of Hunter and Macewicz (1985b). The percentage of fish in the late developing maturity stage with ovaries containing either FOMs or POFs was calculated for each month in each region. This value represents the percentage of the fish in the population that are about to spawn (FOMs) or have just spawned (POFs). Spawning frequency (the number of days between spawnings) was determined by dividing 100 (representing the total population of fish) by the percentage of fish with FOMs or POFs in the ovaries.

Statistical analysis

Student's *t*-test was used to test for differences in GSI values between years. Batch fecundity data were tested for normality and homogeneity of variance. Simple linear regression was used to test the relationship between batch fecundity as the dependent variable and FL or ovary-free body weight as the independent variable. One way analysis of variance was determined for relative batch fecundity. A Mann-Whitney *U* test was used to compare fecundity estimates for the various methods used to determine fecundity. A chi-square test was used to test for differences in spawning frequency among areas. All statistics were computed by using SPSS-PC version 7.5 (SPSS, Inc., 1997) or Systat 8.0 (SPSS, Inc., 1998). Results were considered significant if $P < 0.05$.

Table 1

Numbers of cobia examined histologically from each sampling area.

Area	Males *n*	Months of capture	Females *n*	Months of capture
Southeastern United States (SEUS)	33	February–May	60	February–June
Eastern Gulf of Mexico (EGOM)	43	February–December	60	March–December
North-central Gulf of Mexico (NCGOM)	48	March–October	204	February–September
Western Gulf of Mexico (WGOM)	23	May–August	59	May–August
Totals	147		383	

Results

Fish collections

A total of 530 cobia (147 males, 383 females) from the southern United States were collected for histological analysis. The months and numbers of samples collected varied by region, but in all regions fish were collected primarily during the reproductive season (Table 1). Specimens ranged from 35.5 to 138.5 cm FL for females and 36.5 to 127.0 cm FL for males. Weights ranged from 0.64 to 34.93 kg for females and 0.91 to 40.82 kg for males.

Accurate estimates of the size and age at sexual maturity of cobia from the southern United States could not be determined in this study. Small, immature specimens were rare in recreational catches owing to a minimum retention size of 84 cm FL for cobia in state territorial waters and the EEZ. We collected only six sexually immature specimens (all females from the EGOM) during this study. The smallest reproductively active female encountered was 70 cm FL.

Spawning season and gonadal development

Cobia have a protracted spawning season (April through September) throughout the southern United States as determined from GSI values and histological assessments. There was no significant difference (P>0.05) in GSI values between corresponding months in 1996 and 1997 for either males or females in any region, with the exception of males in September from the NCGOM (P=0.049). Therefore, monthly data for 1996 and 1997 by region were combined (Fig. 2). GSI values for both sexes in SEUS increased sharply from April to May (Fig. 2A), indicating the onset of the reproductive season. GSI values for both sexes of cobia from EGOM began to increase in March, peaked in July, and declined and leveled off thereafter (Fig. 2B). GSI values for females from NCGOM increased in March, peaked in May, and then declined through September (Fig. 2C). In contrast, GSI values of males from NCGOM steadily increased through July, then fell precipitously in August (Fig. 2C). GSI values for males reached similar mean maxima in the SEUS and the NCGOM regions but were lower in the EGOM. However, mean GSI values of females were higher in both May and June for cobia from the SEUS than during any month from the Gulf of Mexico (Fig. 2).

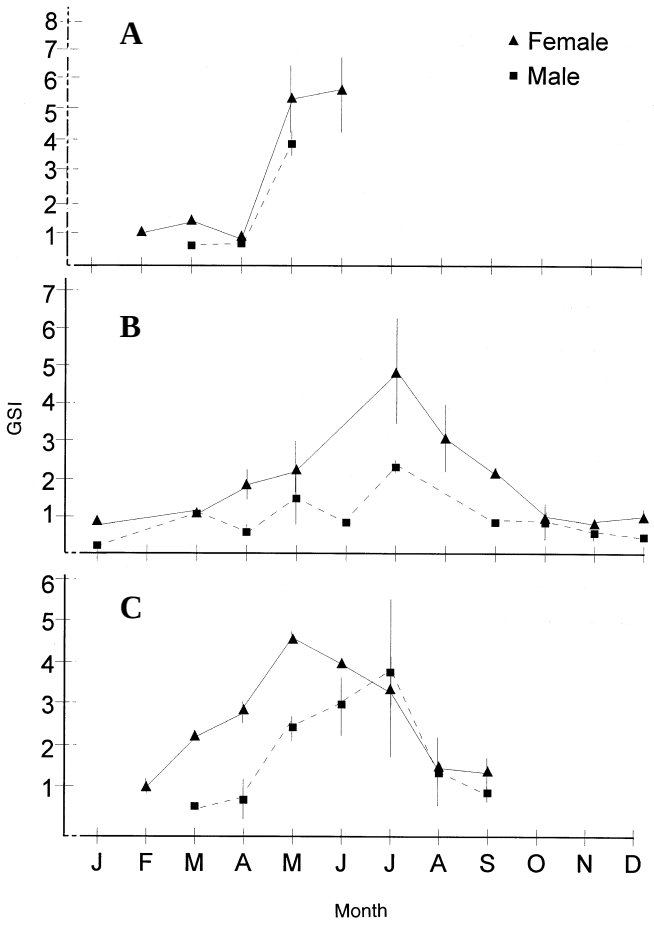

Figure 2

Monthly (1996 and 1997 combined) gonadosomatic index (GSI) values for cobia from the southern United States. Values represent mean ±1SE. (solid triangles=female, solid squares=male) (**A**) Southeastern United States. (**B**) Eastern Gulf of Mexico. (**C**) North-central Gulf of Mexico.

Table 2

Percentage of cobia in each ovarian maturity class for SEUS (Morehead City, NC, to Cape Canaveral, FL). Monthly data from 1996 and 1997 were combined. Percentage atresia was calculated for each development stage for ovaries with alpha- or beta-stage atresia only.

	Month of capture				
Class	February (*n*=3)	March (*n*=31)	April (*n*=10)	May (*n*=10)	June (*n*=6)
Early developing	66	41.9	20	0	0
% atresia	100	92	0	—	—
Mid-developing	34	16	10	0	0
% atresia	100	80	100	—	—
Late developing	0	41.9	70	100	100
% atresia	—	85	66	60	0
Spent	0	0	0	0	0
% atresia	—	—	—	—	—
Regressed	0	3.2	0	0	0
% atresia	—	0	—	—	—

Table 3

Percentage of cobia in each ovarian maturity class for EGOM (Crystal River to Ft. Meyers, FL). Monthly data from 1996 and 1997 combined. Percentage atresia was calculated for each development stage for ovaries with alpha- or beta-stage atresia only.

	Month of capture									
Class	March (*n*=2)	April (*n*=7)	May (*n*=3)	June (*n*=2)	July (*n*=6)	August (*n*=6)	September (*n*=3)	October (*n*=11)	November (*n*=13)	December (*n*=7)
Immature	100	0	0	50	0	16	0	18	7	0
Early developing	0	29	0	0	0	0	0	0	0	0
% atresia	—	50	—	—	—	—	—	—	—	—
Mid-developing	0	14	66	0	0	0	0	0	0	0
% atresia	—	0	50	—	—	—	—	—	—	—
Late developing	0	57	33	50	83	67	33	0	0	0
% atresia	—	50	0	0	0	50	0	—	—	—
Spent	0	0	0	0	17	0	0	18	8	14
% atresia	—	—	—	—	0	—	—	100	100	100
Regressed	0	0	0	0	0	17	66	64	85	86
% atresia	—	—	—	—	—	100	100	86	45	83

Histological analysis showed that all males from all areas were ripe during all months. Spermatogenic activity varied over the reproductive season, but males captured during February–May exhibited active spermatogenesis throughout the testis. No spermatogenesis occurred during August and September, but the testis contained spermatozoa. Males from EGOM during October through December had spermatozoa in the testis, although 50% or more of the males in November and December had the testis classified as spent.

Histological examination of ovaries revealed all classes of maturity, from early developing through regressed. Differences in monthly ovarian maturity between corresponding months in 1996 and 1997 were minimal; thus, monthly data were combined (Tables 2–5). A majority of ovaries from female cobia were in the late developing class by March in the NCGOM (Table 4) and by April in SEUS (Table 2) and EGOM (Table 3). Data from the WGOM (Table 5) were limited to only a portion of the reproductive season. Ovarian recrudescence began in February in the

Table 4

Percentage of cobia in each ovarian maturity class for NCGOM (Destin, FL, to Chandelier Islands, LA). Monthly data from 1996 and 1997 were combined. Percentage atresia was calculated for each developmental stage for ovaries with alpha- or beta-stage atresia only.

	Month of capture							
Class	February (*n*=10)	March (*n*=6)	April (*n*=20)	May (*n*=112)	June (*n*=1)	July (*n*=25)	August (*n*=8)	September (*n*=22)
Early developing	60	0	0	4.5	0	0	0	0
% atresia	60	—	—	20	—	—	—	—
Mid developing	0	33	10	7	0	4	0	0
% atresia	—	100	100	62	—	0	—	—
Late developing	0	67	90	88.5	100	64	37.5	18
% atresia	—	75	44	38	0	31	33	25
Spent	10	0	0	0	0	28	50	23
% atresia	100	—	—	—	—	86	100	80
Regressed	30	0	0	0	0	4	12.5	59
% atresia	0	—	—	—	—	0	0	100

Table 5

Percentage of cobia in each ovarian maturity class for WGOM (Port Aransas, TX) in 1996. Percentage atresia was calculated for each developmental stage for ovaries with alpha- or beta-stage atresia only.

	Month of capture			
Class	May (*n*=1)	June (*n*=8)	July (*n*=48)	August (*n*=2)
Mid developing	0	0	4	50
% atresia	—	—	50	0
Late developing	100	100	73	50
% atresia	0	0	5.7	0
Spent	0	0	21	0
% atresia	—	—	100	—
Regressed	0	0	2	0
% atresia	—	—	100	—

SEUS and the NCGOM, and females in the late developing class occurred in both areas by March (Tables 2 and 4). Spent females were initially observed in July in the Gulf of Mexico (Tables 3–5), although some females remained in the late developing class through September (Tables 3 and 4). Some females in the regressed class occurred in July throughout the Gulf of Mexico (Tables 3–5). In July, lengths of spent and regressed fish ranged from 88.0 to 93.0 cm FL in the EGOM, from 85.5 to 102.1 cm FL in the NCGOM, and from 86.4 to 128.3 cm FL in the WGOM.

Ovarian tissue in all classes of maturity showed atresia throughout the reproductive season. Alpha- and beta-stage atresia of yolked oocytes (Fig. 3A) was most prevalent in spent fish, but also occurred in females in the early, mid and late developing ovarian classes (Tables 2–5). Atresia of hydrated oocytes (Fig. 3B) occurred in ovaries in the late developing and spent classes only (5–10%). Atresia of nonyolked oocytes was difficult to recognize but was common (50–90%) in early developing ovaries. The later stages of atresia (gamma and delta, Fig. 3C) occurred in ovaries in all maturity classes. Many late developing females (60–85%) from the SEUS exhibited alpha- or beta-stage atresia during March through May (Table 2). Similarly, females from NCGOM exhibited high levels of atresia (75%) in ovaries in the late developing class during March (Table 4). Less atresia (38–50%) occurred during April and May in the ovaries of cobia from the Gulf of Mexico (Tables 3 and 4) as compared with cobia from the SEUS (Table 2).

Female cobia underwent final oocyte maturation (FOM) in all four areas sampled during April through September. The early stages of FOM were characterized by early lipid coalescence (Fig. 4A), followed by complete lipid coalescence and migration of the nucleus to the periphery of the oocyte (Fig. 4B). The final stages of FOM, characterized by breakdown of the nuclear membrane, yolk coalescence and hydration, were not observed in any sample. Final oocyte maturation was a synchronous process and most oocytes within an ovary were in the same stage of FOM (Fig. 4C). The percentage of mature oocytes (≥600 µm) undergoing FOM varied from 5% to 84% of the oocytes within a 100× microscopic field of view for all ovaries examined. Females from the EGOM had the highest mean percentage of mature oocytes undergoing FOM (49%). The mean percentage of mature oocytes undergoing FOM was lower, but similar, among the other regions (NCGOM, 19%; SEUS, 16%; WGOM, 15%). The mean percentage of females in the late-developing ovarian class undergoing

FOM ranged from 11% in the WGOM to 59% in the EGOM. On average, 19% of the females from SEUS and NCGOM were undergoing FOM.

The presence of POFs in cobia ovaries indicated spawning had commenced, although POFs were uncommonly observed; the greatest density of POF recorded was five per 100× microscopic field of view. Postovulatory follicles occurred in cobia ovaries in the late-developing class from all regions during April through September, suggesting that although cobia were in the late-developing class by March, spawning commenced in April. The 0-to12-h POF stage (Fig. 5A) was infrequently observed (16%) and was absent in females from the WGOM. The 24-h POF stage (Fig. 5B) was the most frequently observed (51%) and was most common in cobia from EGOM and NCGOM. The 48-h POF stage (33%, Fig. 5C) was difficult to distinguish from gamma- and delta-stage atresia, and most commonly occurred in cobia from theWGOM.

Spawning frequency

Estimates of monthly spawning frequency for the POF and FOM methods (Table 6) were consistent throughout the spawning season in all regions. Both methods showed good agreement for fish from SEUS and NCGOM. The POF method indicated a more frequent estimate of spawning rate in the NCGOM. On the other hand, the FOM method resulted in a more frequent spawning rate for cobia from the WGOM. Cobia from SEUS and NCGOM were estimated to spawn every 4 to 5 days, whereas those from WGOM spawned every 9 to 12 days. Chi-square analysis showed no significant difference in spawning frequency estimates for the three regions for either the POF (P=0.08) or the FOM (P=0.409) method. Months where fewer than five specimens had late developing ovaries were eliminated from the analysis because spawning frequency estimates would probably be inaccurate. No estimate was made for cobia from the EGOM, and spawning frequencies for the WGOM were based on fish captured in July. Spawning frequency estimates for SEUS were based on data from April, May, and June, whereas estimates for NCGOM were based on data from April, May, and July.

Relationship of ovary weight and volume

Direct volume measurements were performed for 86 females with ovarian weights

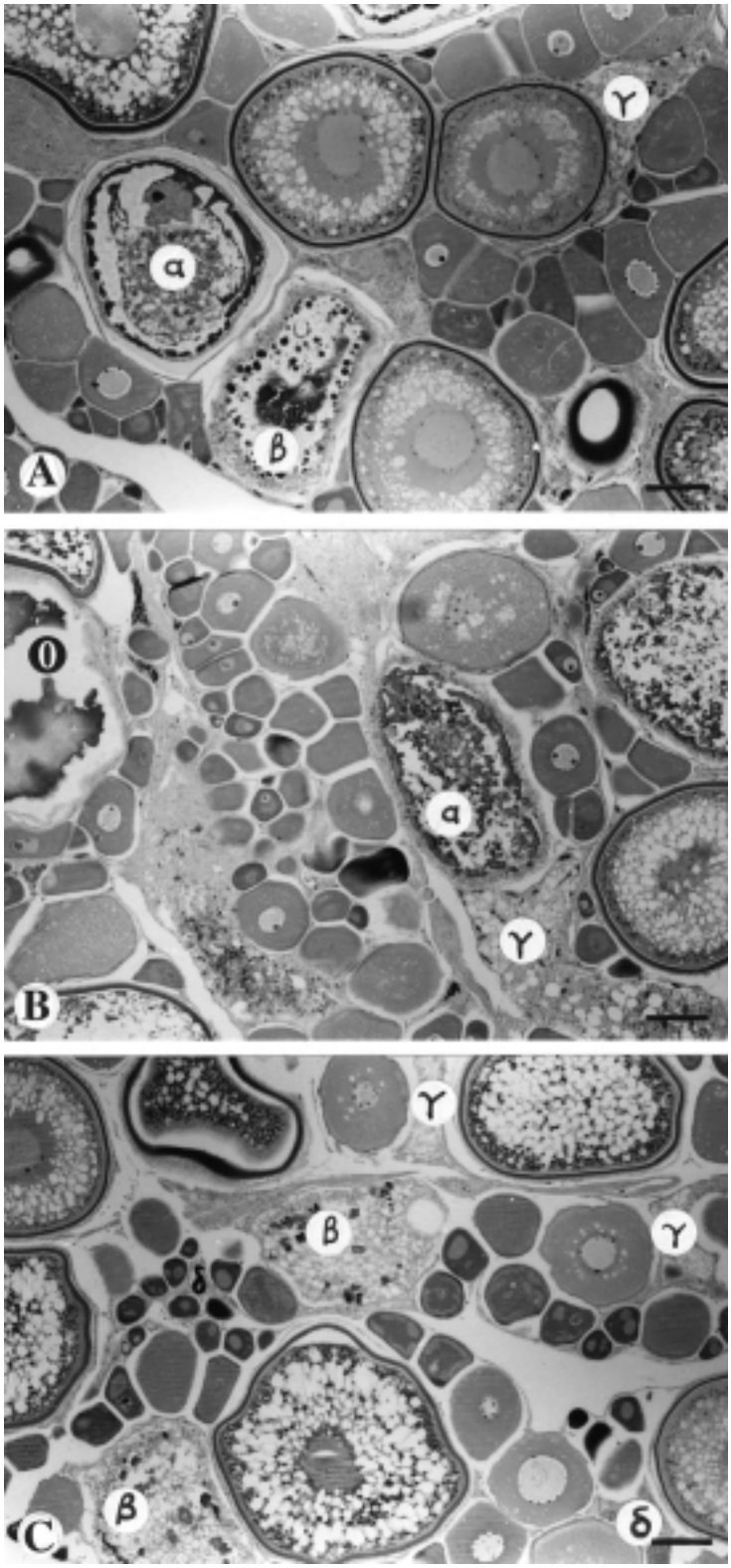

Figure 3

Stages of atresia in cobia ovaries. (**A**) Alpha (α), beta (β), and gamma (γ) stage atresia in a late-developing or spent ovary. Scale bar = 0.1 mm. (**B**) Alpha-stage atresia of a hydrated oocyte (0). Scale bar = 0.1 mm. (**C**) Beta (β), gamma (γ) and delta (δ) stages of atresia in a spent ovary. Scale bar = 0.1 mm.

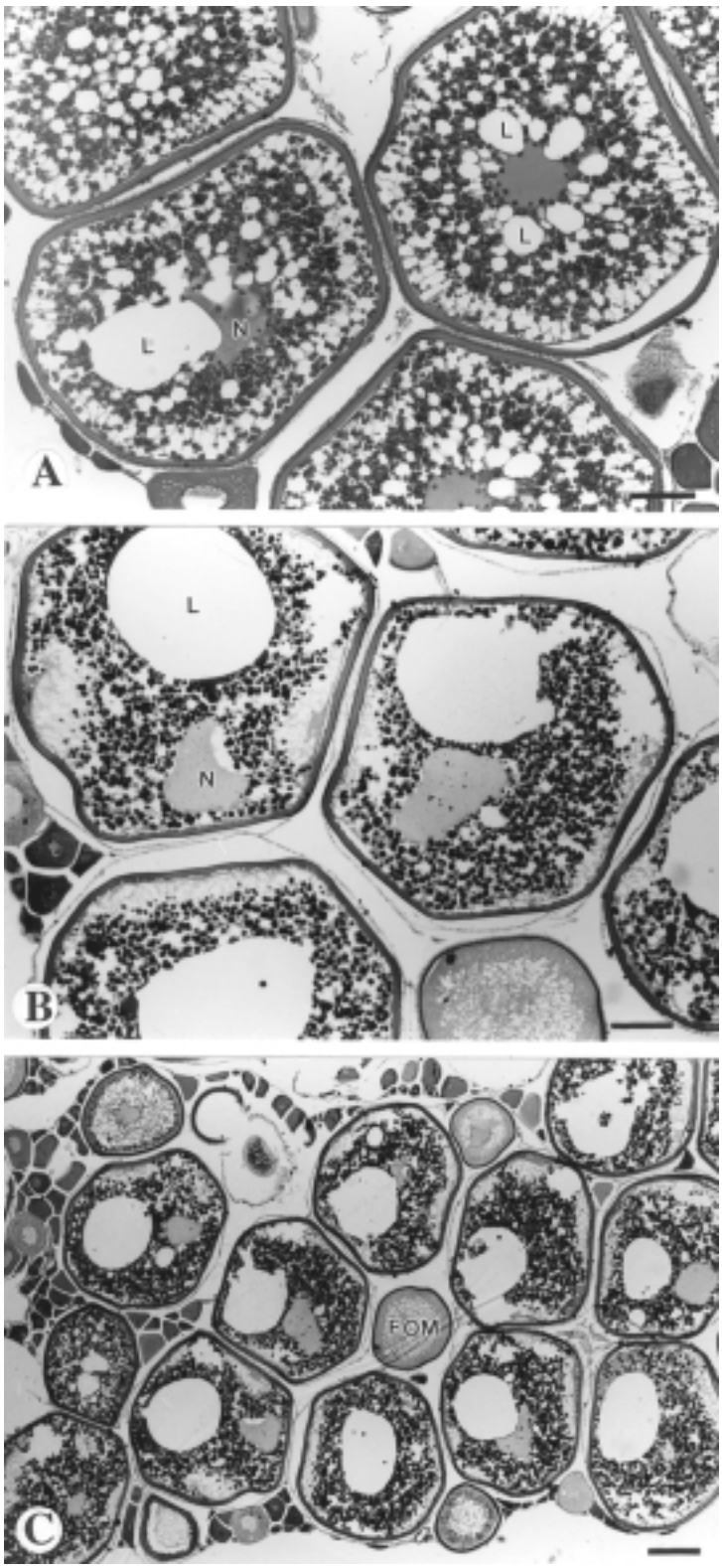

Figure 4

Final oocyte maturation (FOM) in late-developing cobia ovaries. (**A**) Early stage of FOM showing initial lipid coalescence (L). Scale bar = 0.1 mm. (**B**) More advanced stage of FOM. Lipids have coalesced to form a single large droplet (L) and the nucleus (N) is beginning to migrate to the periphery of the oocyte. Scale bar = 0.1 mm. (**C**) Oocytes undergoing synchronous FOM. Scale bar = 0.2 mm.

>500 g. The observed relationship was linear, and the best fit equation as judged by the least squares criterion was mL = –8.54 + 0.96g (r^2=0.978). The relationship indicated that cobia ovaries from 500 to 1600 g were less dense than seawater and that ovary density remained constant over that range.

Batch fecundity

Batch fecundity estimates were compared for samples from 11 females with ovaries fixed in GF, for 40 females with ovaries fixed in NBF, and for 26 ovarian samples examined by the histological method and where oocytes were undergoing FOM from April through September. Samples of this type were limited; therefore we combined observations from SEUS, EGOM, and NCGOM. Fecundity estimates for individual fish varied widely; however, there was no significant difference in mean estimates among the three methods (Mann-Whitney *U*-test, P>0.05; Table 7). Mean batch fecundity ranged from 377,000 ±64,500 eggs (CV=2.677) with the histological method to 1,980,500 ±1,598,500 eggs (CV=0.875) with the GF method.

Batch fecundity estimates for all three methods showed substantial variation. A Kolmogorov-Smirnov test of normality showed that batch fecundity was normally distributed for NBF samples (40 df, P>0.05) and FOM samples (26 df, P>0.05) and could be analyzed by using parametric statistics. Batch fecundity determined with the GF method was not used for further analyses owing to the small sample size. Regression analysis showed a significant, positive relationship between batch fecundity (BF) and FL (P=0.021, r^2=0.132) and BF and ovary-free body weight (OFBW; P=0.016, r^2=0.143) for NBF samples. The relationship between BF and OFBW for NBF samples (Fig. 6A) was described by

$$BF = OFBW^{1.717} - 36.813.$$

There was no significant relationship between BF and FL (P=0.105) or OFBW (P=0.097) for FOM samples. The relationship between BF and OFBW for FOM samples (Fig. 6B) was described by

$$BF = 19.29 \times \text{OFBW} + 1{,}113{,}713 \quad [r^2=0.11,\ P=0.097].$$

Mean batch fecundity, as determined from the NBF method, averaged 854,100 ±166,200 eggs and ranged from 247,100 ±204,400 eggs in August (n=2) to 923,000 ±237,700 eggs in May (n=26). Mean batch fecundity, as

determined with the FOM method, averaged 377,000 ±64,500 eggs and ranged from 212,500 ±122,700 eggs in August (n=5) to 637,000 ±376,600 eggs in September (n=3) .

Relative batch fecundity (Table 8) did not vary significantly from April through September as determined by the NBF method (F=0.636, df=37, P=0.639) and the FOM method (F=0.468, df=24, P=0.759). Relative batch fecundity for the NBF method averaged 53.1 ±9.4 eggs/g ovary-free body weight throughout the reproductive season (n=39, Table 8) and it was lowest in August and highest in June. Relative fecundity values determined with the FOM method were lower than those with the NBF method, averaging 29.1 ±4.8 eggs/g ovary-free weight (n=25, Table 8), and were lowest in June and highest in July.

Potential annual fecundity for cobia was estimated from batch fecundity and spawning frequency estimates. A female cobia weighing 20 kg from SEUS or NCGOM may potentially spawn 20,952,000 (FOM method) to 38,232,000 (NBF method) eggs between April and September. In contrast, the same size female from WGOM would potentially spawn 8,730,000 (FOM method) to 21,240,000 eggs (NBF method) between April and September, with the data provided here.

Discussion

Our data show that the reproductive biology of cobia is similar throughout the coastal waters of the southern United States. Although sample sizes from some regions and months were small due to reliance on recreational catches for samples, we feel the data adequately represent the reproductive population from the four regions. Spawning commences in April throughout the region, as evidenced by the presence of oocytes undergoing FOM as well as 24-h POFs. These findings are in agreement with previous studies of cobia reproduction in the southeastern U.S. Atlantic Ocean (Smith, 1995) and the north-central Gulf of Mexico (Biesiot et al., 1994; Lotz et al., 1996; Thompson et al.[2]). Collections of larval cobia from the Gulf of Mexico during May through September (Ditty and Shaw, 1992) also confirm the spawning season. Reproductive activity of female cobia probably ceases during September in the Gulf of Mexico and extends at least through June in the SEUS. Smith (1995) reported that cobia from North Carolina spawned through July. Eggs and larvae

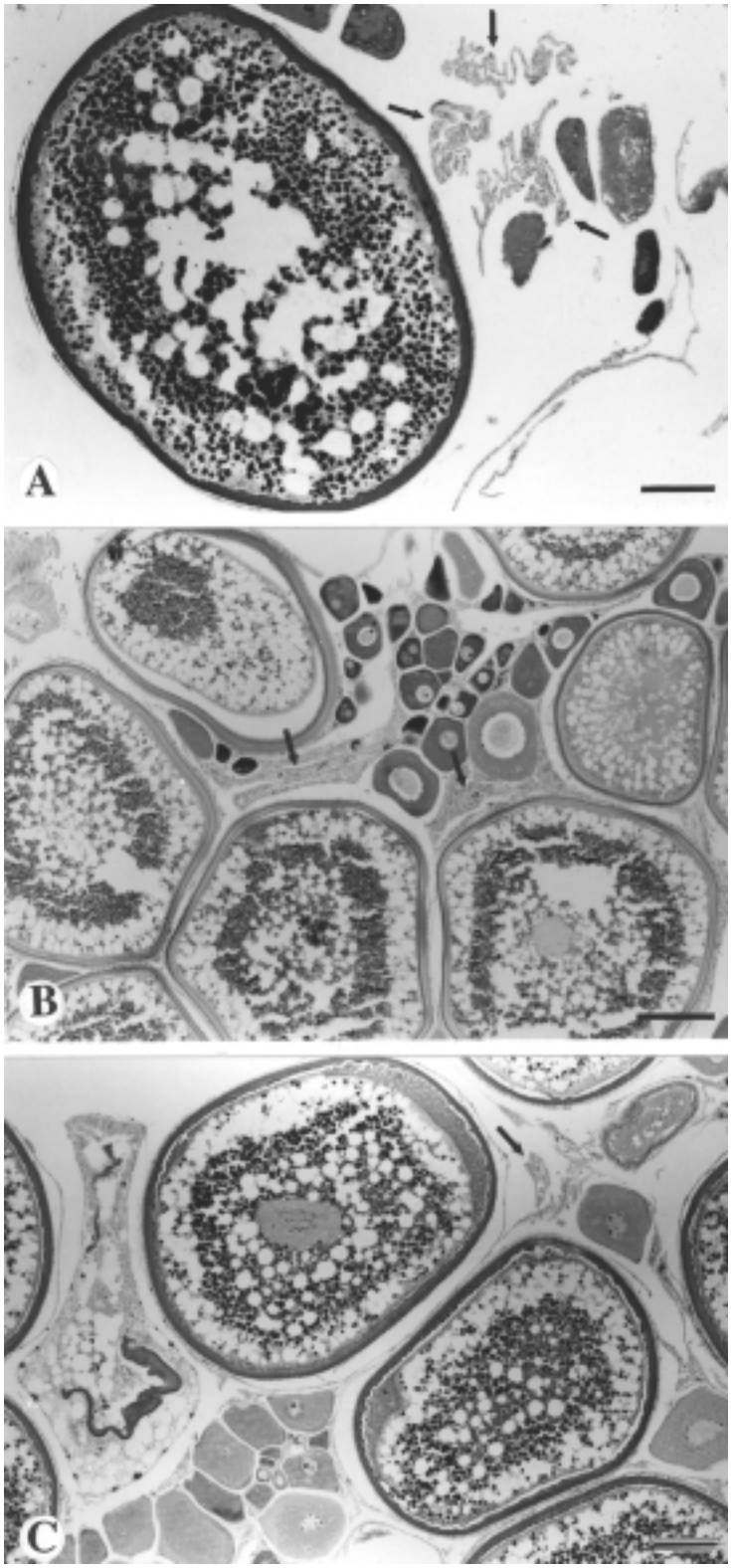

Figure 5

Postovulatory follicles (POF) in late-developing cobia ovaries. (**A**) 0- to 12-h POF (arrows). Scale bar = 0.1 mm. (**B**) 24-h POF (arrows). Scale bar = 0.2 mm. (**C**) 48-h POF (arrow). Scale bar = 0.1 mm.

Table 6

Mean estimated spawning frequencies of cobia from three regions in the southern United States. Spawning frequencies are estimated from the percentage of ovaries in the late developing ovarian class containing either postovulatory follicles (POF) or undergoing final oocyte maturation (FOM). Spawning frequency estimates were based on data from April to June in SEUS, from April, May, and July in NCGOM, and during July in WGOM.

	Region		
Spawning frequency	Southeastern United States (SEUS) (*n*=23)	Northcentral Gulf of Mexico (NCGOM) (*n*=135)	Western Gulf of Mexico (WGOM) (*n*=35)
% POFs	19.4	24.8	8.1
Frequency (POFs)	5.2 days	4.0 days	12.3 days
% FOM	19.4	19.8	10.8
Frequency (FOM)	5.2 days	5.0 days	9.2 days

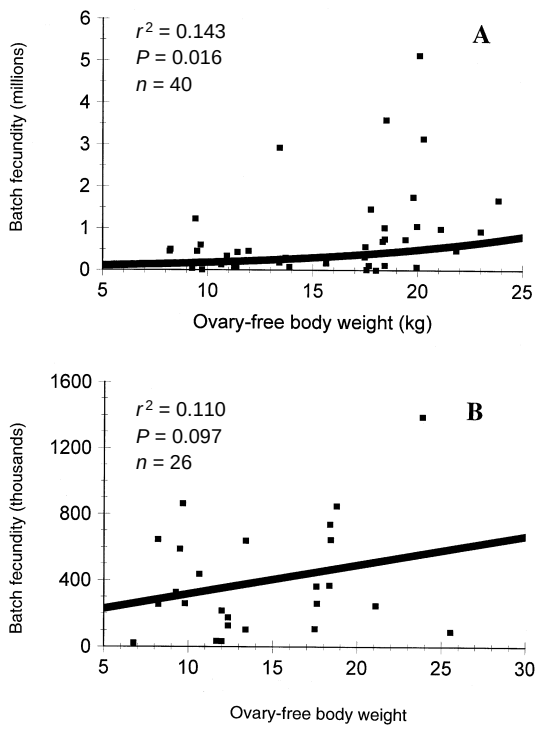

Figure 6

Relationship between batch fecundity (BF) and ovary-free body weight (OFBW) for cobia from the southern United States. Cobia were captured from April through September of 1996 and 1997 from the southeastern United States, the eastern Gulf of Mexico, and the north-central Gulf of Mexico. (**A**) Batch fecundity determined from formalin-fixed oocytes >700 µm. $BF = OFBW^{1.717} - 36.813$. (**B**) Batch fecundity determined from histological sections of oocytes undergoing final oocyte maturation. $BF = 19.29O \times OFBW + 1{,}113{,}713$.

Table 7

Batch fecundity estimates (no. of eggs) of cobia from the southern United States determined with three different methods. All means were not statistically different (Mann-Whitney *U*-test, *P*>0.05). NBF = neutral buffered formalin. FOM = final oocyte maturation.

	Fecundity method		
Measurement	Gilson's fixative (*n*=11)	10% NBF (*n*=40)	Histology (FOM) (*n*=26)
Percentage of ovary counted	0.02	0.02	0.005
Mean number of eggs	1,980,500	854,000	377,000
Standard error	1,598,500	166,200	64,500
Coefficient of variation	2.677	1.246	0.873
Minimum number of eggs	2,700	8,000	22,900
Maximum number of eggs	17,848,800	5,132,000	1,390,000

of cobia were collected from the Chesapeake Bay from mid-June through mid-August (Joseph et al., 1964), whereas cobia eggs from North and South Carolina were collected from mid-May through the end of August (Hassler and Rainville, 1975; Shaffer and Nakamura, 1989).

Gonadosomatic index values are indicators of the duration of the reproductive season for cobia, and they correlated well with our histological findings. However, Jons and Miranda (1997) advised caution in their use because of regional and temporal variations in GSI values. Therefore, GSI values should not be used for comparing or indexing

Table 8

Monthly mean relative batch fecundity expressed as number of eggs/g ovary-free body weight for cobia in the southern United States. Batch fecundity was determined from oocytes >700 µm in neutral buffered formalin (NBF) and from histological sections of oocytes undergoing final oocyte maturation (FOM). All means were not statistically different (ANOVA, $P>0.05$).

	NBF		FOM	
Month	*n*	Relative fecundity ±1SE	*n*	Relative fecundity ±1SE
April	1	46.6	0	—
May	25	51.2 ±12.2	8	24.6 ±4.9
June	2	115.7 ±102.2	3	21.9 ±12.9
July	5	44.0 ±9.2	6	40.2 ±12.9
August	2	29.8 ±25.2	5	24.6 ±14.9
September	4	57.7 ±27.5	3	33.2 ±13.0
Overall	39	53.1 ±9.4	25	29.1 ±4.8

maturity stages, particularly in multiple spawning fish. The GSI profile for both male and female cobia from the SEUS is similar to that described by Smith (1995) for cobia from North Carolina. On the other hand, GSI peaks for cobia from the northern Gulf of Mexico vary among studies. Biesiot et al. (1994) reported that female GSI values peaked in April, Lotz et al. (1996) found peak female GSI values in May, and Thompson et al.[2] reported peak female GSI values in June. Our data for females mirror those presented by Lotz et al. (1996); however, we suspect annual differences.

Our study was not designed to determine the size or age at first maturity for cobia. However, our limited data suggest that both sexes of cobia may achieve sexual maturity at a smaller size than that reported by Lotz et al. (1996) for the north-central Gulf of Mexico. This apparent difference in the size at sexual maturity could be partially explained by regional differences; most small female cobia in the present study (<85 cm FL) were captured in EGOM, whereas Lotz et al. (1996) sampled in NCGOM.

Male cobia are probably capable of spawning throughout the year because of the presence of sperm in the testis. A more detailed analysis of the histological pattern and spermatogenesis of male cobia will be discussed separately (Brown-Peterson et al.[4]). A similar longer reproductive season for male fish has been reported for other species with protracted spawning seasons including common snook (*Centropomus undecimalis*, Grier and Taylor, 1998; Taylor et al., 1998), spotted seatrout (*Cynoscion nebulosus*, Brown-Peterson et al., 1988), red drum (*Sciaenops ocellatus*, Grier et al., 1987), and blue tilapia (*Oreochromis aureus*, Grier and Abraham, 1983).

Cobia have a protracted spawning season, yet a portion of the females in the population may spawn during April–June only. Other females remain in spawning condition throughout September in the Gulf of Mexico. Lotz et al. (1996) and Biesiot et al. (1994) reported a similar occurrence in cobia from the NCGOM, and a high percentage of female cobia off Louisiana are spent and regressed by July (Thompson[5]). A comparable phenomenon, i.e. asynchronous cessation of spawning, was reported in the weakfish (*C. regalis*) in Chesapeake Bay (Lowerre-Barbieri et al., 1996). It is difficult to explain early cessation of spawning by some female cobia. Spent and regressed fish in July and August had a broad length distribution (85 to128 cm FL), suggesting that multiple age classes in the fishery have an abbreviated reproductive season. Perhaps some females delay ovarian maturation and spawn between July and September; this theory would account for the small percentage of females in the early- and mid-developing classes in May and June.

Differences in the amount of oocyte atresia during the spawning season between cobia from the SEUS and the Gulf of Mexico suggest differential spawning success during the early portion of the reproductive season. High percentages of alpha and beta atresia in cobia in the late-developing class from SEUS during March, April, and May suggest that many oocytes do not reach final maturation and that the atresia may be related to variable or unfavorable environmental conditions during spring (March–May) in the region. Hay and Brett (1988) showed a similar occurrence for Pacific herring (*Clupea harengus pallasi*) of increased atresia at the beginning of the reproductive season—condition they attributed to environmental factors rather than the female's physiological ability. Lowerre-Barbieri et al. (1996) used similar reasoning to explain the increased percentage of alpha and beta atresia present in the ovaries of weakfish captured during the beginning of the spawning season in Chesapeake Bay. Cobia from NCGOM also showed high percentages of atresia during March, the beginning of the reproductive season but prior to the initiation of spawning in that area. The lower percentage of females in the late-developing class with atretic oocytes in the Gulf of Mexico during April and May suggests a relatively high spawning success during the early portion of the spawning season in the Gulf of Mexico, and it also may suggest more stable environmental conditions in this region during late spring.

In the absence of hydrated oocytes in any cobia that we or Lotz et al. (1996) examined, we used three different methods to estimate fecundity of cobia containing large (>700 µm) oocytes. The wide range of results found among methods highlights the variations to be expected when estimating batch fecundity of a multiple spawning species.

[4] Brown-Peterson, N. J., H. J. Grier and R. M. Overstreet. 2000. Manuscript in preparation. Reproductive classes in male cobia (*Rachycentron canadum*) defined by changes in the germinal epithelium. Abstract and presentation at the 80th annual meeting of the American Society of Ichthyologists and Herpetologists, June 2000, La Paz, B.C.S., Mexico.

[5] Thompson, B. A. 1999. Personal commun. Coastal Fisheries Institute, LSU Center for Coastal, Energy and Environmental Resources, Baton Rouge, LA 70803.

It is reasonable to assume that a female will not always spawn the same number of oocytes during each spawning event and that this variation in batch size may not be related to body size, as indicated for fecundity estimates with the FOM method. Furthermore, although only large oocytes were counted with the GF and NBF methods, not all females with oocytes >700 µm underwent FOM, as determined by histological inspection. Because histological inspection is not always practical when fecundity estimates are taken, we feel our estimates should include all fish with oocytes >700 µm. Both the GF and NBF methods resulted in higher, but not significantly different, fecundity estimates than those yielded by the histological method, suggesting that the wide variation among individual fish obscures any meaningful difference among methods.

We believe our most accurate fecundity estimates are based on the actual histological counts of oocytes undergoing FOM. Our approach is supported by Hunter and Macewicz's (1985b) finding that oocytes undergoing FOM can be used for fecundity estimates in fish with rapid FOM when hydrated oocytes are unavailable. Although the exact time frame of FOM is unknown for cobia, we presume it is relatively rapid. For example, fish in the early stages of FOM were captured in the morning. Cobia are presumed to spawn during the day, probably the late afternoon, on the basis of collections of fertilized eggs (Ditty and Shaw, 1992). Other multiple spawning fish from similar latitudes (e.g. *C. nebulosus* [see Brown-Peterson et al., 1988], black drum, *Pogonias cromis* [see Fitzhugh et al., 1993], and *C. undecimalis* [see Taylor et al., 1998]) undergo FOM within 12 h. Several large scombrids also have rapid FOM (McPherson, 1993; Schaefer, 1996; Farley and Davis, 1998). From this evidence, we conclude that accurate batch fecundity estimates can be made for cobia by using oocytes from fish undergoing FOM.

The estimated mean batch fecundity values from the present study (1.9×10^6 eggs with the GF method, 8.5×10^5 with the NBF method, and 3.8×10^5 with the histologic method) are lower than previous mean estimates by Lotz et al. (1996) of 4.8×10^7 and Richards (1967) of 2–5 $\times 10^6$ eggs. Differences in methods no doubt explain the wide range in estimates. We used only oocytes >700 µm for fecundity estimates rather than all oocytes >550 µm used by Lotz et al. (1996) and Richards (1967). Our methods ensured that only oocytes likely to undergo hydration within the following 24 h were included in fecundity estimates. Lotz et al. (1996) suggested that their batch fecundity values may have been an overestimate because all the oocytes counted may not have been released during spawning. Richards (1967) probably also overestimated the batch fecundity of cobia, although his estimates are close to ours obtained by using the GF method.

Batch fecundity was not estimated for any species by using direct histological counts of oocytes undergoing FOM; thus, it is difficult to compare our results with other published results. Even though the estimates appear low when compared with more traditional methods of estimating fecundity, there is less variation in the counts. The relatively small sample size (n=26) used in our study for the FOM method may have resulted in an underestimation of batch fecundity. Increasing the sample size from <30 to 298 fish resulted in an increase as great as 33% in batch fecundity estimates for Atlantic mackerel *(Scomber scombrus*, see Watson et al., 1992). Although our batch fecundity estimates for cobia are realistic first approximations, additional samples are necessary to produce a more accurate mean estimate of batch fecundity, a crucial value for accurate spawning stock biomass assessments. In addition, the large variations in batch fecundity among individual fish are probably a biologically accurate representation of variations in batch size in this multiple spawning species. Thus, assigning a single value to the batch fecundity of cobia does not give a biologically accurate portrayal of spawning stock biomass.

The mean relative fecundity of 29.1 ±4.8 to 53.1 ±9.4 eggs/g ovary-free body weight calculated for cobia is low when compared with co-occurring inshore and estuarine fish in the region (Brown-Peterson et al., 1988; Fitzhugh et al., 1993). Cobia, like the co-occurring tripletail (*Lobotes surinamensis)*, wahoo (*Acanthocybium solandri*), common dolphinfish *(Coryphaena hippurus*), king mackerel (*Scomberomorus cavalla*), and greater amberjack (*Seriola dumerili*), is a large, subtropical pelagic fish and exhibits a very different life history than smaller nearshore and estuarine species. Fecundity data are available only for two of these co-occurring species: wahoo, with an estimated relative fecundity of 57.7 eggs/g (Brown-Peterson et al., 2000) and tripletail, with an estimated relative fecundity of 47.6 eggs/g (Brown-Peterson and Franks, in press). Values from both species compare favorably with our estimates for cobia. Other pelagic species for which relative batch fecundity values are available include Atlantic mackerel (55.5 eggs/g; Watson et al., 1992), southern bluefin tuna (*Thunnus maccoyii*, 57 eggs/g; Farley and Davis, 1998) and yellowfin tuna *(Thunnus albacares*, 68 eggs/g; Schaefer, 1996). When the relative fecundity of the cobia is compared with that of other species with similar habitats and life histories, our estimate appears within the range of reported values for other pelagic species.

Our study represents the first report of spawning frequency for cobia. The FOM and the POF methods produced estimates of spawning at five-day intervals for cobia in the SEUS and NCGOM. However, these estimates are based on three months of data for a potential six-month spawning season and thus may not represent the spawning frequency throughout the entire reproductive period for each region. Regardless, this spawning frequency is lower than that reported for other large pelagic species, such as narrow barred Spanish mackerel (*S. commerson*, 2–3 d, McPherson, 1993), southern bluefin tuna (daily spawners, Farley and Davis, 1998), yellowfin tuna (1–2 d, Schaefer, 1996) and wahoo (2–6 d, Brown-Peterson et al., 2000), as well as for the smaller pelagic carangids (3 d, Clarke and Privitera, 1995), spotted seatrout (2–7 d, Brown-Peterson et al., 1988), common snook (1.1–2.5 d, Taylor et al., 1998), and red drum (2–4 d, Wilson and Neiland, 1994). Perhaps, the longer intervals between spawnings for cobia may be due to the longer distances that cobia need to travel between feeding and spawning grounds in comparison with the distances traveled by the

species just mentioned. The exact location of cobia spawning is unknown; early surveys have suggested spawning immediately outside the mouth of Chesapeake Bay (Joseph et al., 1964), whereas later data from the southeastern United States have indicated that cobia spawn offshore of North Carolina (Hassler and Rainville, 1975) and South Carolina (Shaffer and Nakamura, 1989). Egg collections in Crystal Bay, FL (Ditty and Shaw, 1992), imply that spawning occurs nearshore in the Gulf of Mexico, although other egg and larval evidence (Shaffer and Nakamura, 1989; Ditty and Shaw, 1992) suggest spawning occurs in the Gulf of Mexico on the shelf 50–90 km from shore. Further evidence for offshore spawning was the collection of small larvae (3.8–6.8 mm) 50–90 km off the coast of Texas (Finucane et al.[3]). Because most of our samples were captured no more than 40 km from shore, cobia in immediate pre- or postspawning condition may not occur in those locations. In addition, our hook-and-line method of capture may be biased against cobia in immediate pre- or postspawning condition owing to changes in feeding behavior at these stages.

Although spawning frequencies of cobia from the three study areas were not significantly different, the apparent lower spawning frequency of cobia in the WGOM may be biologically relevant. Cobia from SEUS and NCGOM were estimated to be capable of spawning up to 36 times during the six-month spawning season, whereas fish from WGOM were estimated as capable of spawning 15 to 20 times during the spawning season. Hydrologic features of the areas may explain the differences. The southeastern United States and the north-central Gulf of Mexico have substantial inputs of freshwater from major river systems which may result in high productivity in those areas (Livingston et al., 1997) and hence abundant food sources. In contrast, there is little freshwater input along the western Gulf of Mexico.

Another possible explanation for the differences in spawning frequencies may be that many cobia in the Gulf of Mexico spawn in a single location that is closer to the north-central region than to the western region. The lack of 12-h POFs and the predominance of 48-h POFs seen in the ovaries of cobia from the western Gulf of Mexico may be due to the longer distance that western cobia must travel from the spawning grounds. This hypothesis assumes that cobia in the Gulf of Mexico do not have distinct breeding areas or subpopulations—a hypothesis supported by Hrincevich's (1993) work on the molecular genetics of cobia. Although Hrincevich (1993) did find a high degree of heterogeneity in cobia mtDNA, this heterogeneity did not support the hypothesis that discrete stocks of cobia exist in the northern Gulf of Mexico. The genetic data, in combination with data from tagging studies in the northern Gulf of Mexico (Franks et al.[6]), suggest that cobia intermix not only within the Gulf of Mexico but also along the southeastern Atlantic coast of the United States. Thus, the overall similarities in the reproductive biology of cobia throughout the southern United States are not surprising. The information provided in our study on batch fecundity and spawning frequency of cobia should aid effective management of cobia stocks, as well as underscore areas where additional research is needed.

[6] Franks, J. S., J. T. McBee, and M. T. Allen. 1992. Studies on the seasonal movements and migratory patterns of the cobia, *Rachycentron canadum*, in Mississippi marine waters and adjacent Gulf waters. Interim Contract Rep. to Miss. Dep. Wildl., Fish, and Parks/Bur. Mar. Res, and U.S. Fish and Wildl. Serv, Atlanta, GA 30303. [Available from Gulf Coast Res. Lab., Ocean Springs, MS 36566-7000.]

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