Ovarian development, fecundity, and spawning frequency of black drum *Pogonias cromis* in Louisiana

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Abstract.—Patterns in oocyte development, batch fecundity, and spawning frequency were assessed for black drum *Pogonias cromis* from Louisiana. We identified histological oocyte stages present throughout a protracted breeding season in 1986–87. We observed vitellogenesis beginning in November, and first postovulatory follicles were detected in February. Atresia of yolked oocytes was complete in May. We detected recruitment of vitellogenic eggs after the onset of spawning, suggesting indeterminant total fecundity. Mean batch fecundity for a 6.1 kg female (mean size sampled with hydrated oocytes) was calculated to be 1.6 million hydrated oocytes. A field estimate of spawning frequency was 0.311, indicating that a female spawns on average once every 3 d during the breeding season. Sex ratios were skewed with respect to sampling gear during the breeding season, suggesting segregation of actively-spawning fish on the spawning grounds.

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The black drum *Pogonias cromis* ranges from Argentina to the Bay of Fundy (Sutter et al. 1986) and is the largest sciaenid, up to 66 kg (Hildebrand & Schroeder 1928). A maximum age of 43 yr was recorded for black drum in the northern Gulf of Mexico (Beckman et al. 1990). Fishing pressure on black drum was historically very low, but has increased with commercial landings in the Gulf of Mexico rising from 1.9 million kg in 1982 to 4.8 million kg in 1987 (NMFS Natl. Fish. Stat. Office, New Orleans LA 70130).

Many temperate fishes are serial spawners with variable production of clutch sizes (Hunter & Goldberg 1980, DeMartini & Fountain 1981, Conover 1985). In particular, large long-lived species may exhibit high variability in reproductive output (Ware 1982). An important management objective with long-lived species is to identify changes in population egg production associated with the harvest loss of older age-classes. For black drum, the potential for exploitation of older age-classes is increased with development of the commercial fishery (NMFS 1986).

Despite the commercial value of black drum, relatively little is known of many life-history aspects of this species (Sutter et al. 1986). In the northern Gulf of Mexico, the spawning season has been reported from late-fall to spring, based upon egg and larval distributions (Jannke 1971, Holt et al. 1985, Ditty 1986) and occurrence of gravid females (Cody et al. 1985). Peters & McMichael (1990) reported peak spawning in March from Tampa Bay, Florida, based on distribution of larvae and juveniles. Murphy & Taylor (1989) computed size-at-maturation to be 590 mm and 650 mmFL for males and females, respectively, although there have been accounts of small females (<350 mmFL) with developing ovaries (Simmons & Breuer 1962, Pearson 1929). Spawning locations have been reported to occur within estuarine bays and in open coastal waters (Pearson 1929, Simmons & Breuer 1962, Jannke 1971, Peters & McMichael 1990). There has been only one estimate of fecundity determined from a single female (Pearson 1929), and no previous estimate of spawning frequency has been made from the adult stock.

Our objective is to provide baseline reproductive information from 1986–87 to be used in assessing popula-

tion changes and potential egg production to maintain future fishing harvests. We characterize ovarian development, seasonal spawning duration, and frequency as determined by ovarian histology and batch fecundity in Louisiana coastal waters.

Materials and methods

We sampled black drum monthly from commercial landings during March, June, July, October, November, and December 1986 and July 1987 to obtain reproductive information. We increased sampling effort during the period of reported peak seasonal reproductive activity and sampled 25 commercial landings during February, March, April, May, and June 1987. We also sampled recreational hook-and-line landings during March and July 1986 and April 1987. Landings sampled from inshore waters (bays and sounds) were primarily taken by gillnet, haul-seine, and hook-and-line. Landings sampled from offshore waters were taken by trawl and purse-seine.

In order to contrast size-at-maturity with other studies, we made gross visual classifications of gonads during sampling. Macroscopic characteristics for classifying gonads as mature correspond to Bagenal (1968) and Nielson & Johnson (1983). Female characteristics included the presence of eggs visible to the naked eye and light-yellow to reddish appearance from increased vascularization of the ovary. Characteristics for mature males included white appearance and relative enlargement of testes within the body cavity. Measurements included fork length (FL), sex, gutted (viscera removed) body weight (BW), and gonad weight (GW; wet weight blotted dry to nearest 0.1 g). We documented reproductive development by expressing gonad weight as a function of body size using the gonosomatic index (GSI) (Htun-Han 1978, Nielson & Johnson 1983).

We held gonads in ice up to 24 h after sampling and then fixed gonads in 10% formalin. One tissue sample was randomly selected from the preserved ovary and placed in an OmniSette tissue cassette. For histological observation, tissue samples were dehydrated, embedded in paraffin, sectioned, stained with Gill's hematoxylin, and counter-stained with eosin*. We classified oocytes from the prepared histology slides following Wallace & Selman (1981), DeVlaming (1983), and Selman & Wallace (1986). These stages include primary growth (PG), cortical alveoli (CA), vitellogenesis (V), and hydration (H).

To determine relative frequency of oocyte stages, we located a random starting point on a histological section and counted and staged all identifiable oocytes within a field before moving to a new microscope field using manual stage drive. Field movement was inward along the ovigerous lamellae, from the outer tunica albuginea toward the center of the ovary, with realignment along a vertical axis. To be counted, >50% of an oocyte must have been within a field of view. We counted and staged a minimum of 200 oocytes from each female and expressed tallies of the four oocyte stages as a percentage of the total count (Htun-Han 1978, Holdway & Beamish 1985). The Bioquant IV image analysis system software, IBM PC, and Houston Instrument digitizing pad (Hipad model DT-11) were used in conjunction with an Olympus microscope (with video attachment) to facilitate counts and measurements.

In addition to relative frequency of developmental stages, we classified each histological section for the presence of postovulatory follicles (POF) and atretic oocytes to aid in determination of spawning frequency. Our atresia classification was modified from that for northern anchovy (Hunter & Macewicz 1985). If no atresia of yolked oocytes was observed, we denoted the ovary as atretic state 0. Tissue sections exhibiting yolked oocytes undergoing atresia at <50%, >50%, and 100% were classed as atretic states 1, 2, and 3, respectively.

To estimate oocyte development rate, we related our histological observations of actively-spawning black drum to published accounts of spawning time of black drum (Mok & Gilmore 1983, Holt et al. 1985) and rates of hydration and postovulatory follicle degeneration in sciaenids (DeMartini & Fountain 1981, Brown-Peterson et al. 1988). With this time-calibrated histological information, we estimated the hours from spawning for females displaying yolk coalescence, hydration, postovulatory follicles, and atresia, and classified day-0, day-1, and nonspawning females. Our estimate of seasonal spawning frequency was determined by taking the average of the fractions of day-0 and day-1 spawning females relative to total females observed histologically with vitellogenic oocytes. Batch fecundity, the number of hydrated oocytes which comprise the leading "batch" of eggs immediately prior to spawning, was determined from formalin-fixed tissue samples taken from each visibly-hydrated ovary. We took replicate ovarian tissue samples (1–2 g) from anterior, mid-, and posterior regions of left and right lobes. In order to obtain 100–300 hydrated oocytes, tissue subsamples of 90–100 mg (weighed to the nearest 0.05 mg) were placed on a slide, glycerin added, and hydrated oocytes counted (Hunter et al. 1985). After observation of histological sections, any ovaries

* Preparation of histological slides, including washing, embedding, sectioning and staining, were completed by the Louisiana State University School for Veterinary Medicine, Department of Pathology.

with postovulatory follicles, indicating onset of spawning and possible shedding of eggs, were eliminated from further analysis of fecundity. To determine the precision of batch fecundity methodology (Hunter et al. 1985), we compared oocyte counts per unit weight within ovaries using a two-way analysis-of-variance model, SAS GLM procedure (SAS 1985).

Results

Sampling, sex ratio, and maturity

We recorded information on length, sex, and gear for 236 male, 108 female, and 36 immature black drum. In addition, we collected capture data, ovarian samples, and measurements, including somatic and gonad weights used for GSI analysis, from 198 males and 296 females. Ovarian histology sections were made from 234 mature females randomly sampled through June 1987, and were used to determine relative frequencies of oocyte stages (Fig. 1). Of these females, 25 were visibly hydrated, possessed no postovulatory follicles, and were used to estimate batch fecundity. Our sample mean length was 761 mmFL, with adults measuring 650–900 mmFL comprising 89% of individuals used in the study.

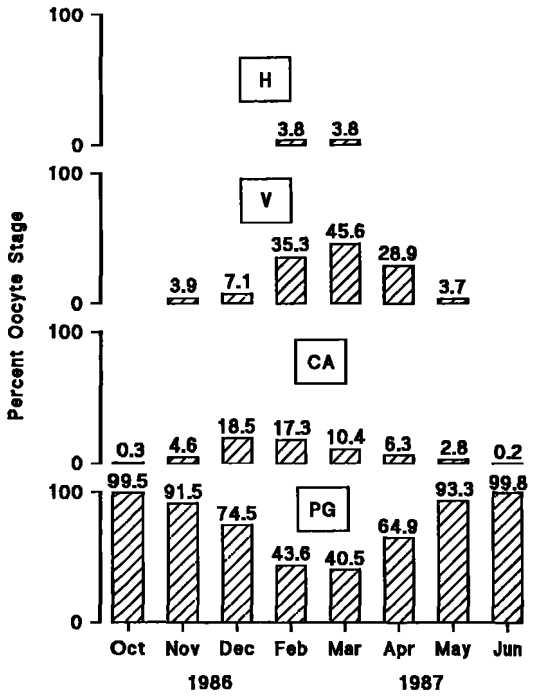

Figure 1

Percent oocyte stage by month for 1986–87 based on point counts of ~200 oocytes/female black drum *Pogonias cromis*. Stages include primary growth (**PG**), cortical alveolar (**CA**), vitellogenic (**V**), and hydrated (**H**). Number of females examined = 22 Oct, 23 Nov, 23 Dec, 69 Feb, 32 Mar, 24 Apr, 22 May, 19 June.

We found apparent differences in sex ratios from inshore landings (gillnet and haul-seine) and landings from an offshore trawl fishery during the reproductive season (Table 1). Trawl catches were dominated by males, while gillnet and haul-seine samples were dominated by females (Table 1). For months just before and after the reproductive season (October, June, July), females also dominated gillnet and haul-seine landings, but ratios were less divergent. The trawl fishery was not active at these times, but samples of offshore fish were taken from a purse-seine landing (June 1986) and numbers of females and males were nearly equal (0.92:1.0). We applied a χ^2 contingency analysis to test sex ratios by gear type. The χ^2 statistic was significant during the reproductive season (December–May), leading to rejection of the null hypothesis that gear type and sex ratio are independent (Table 1). We assumed that gears were not selective for sex but reflected actual sex ratios in the localities fished. Therefore, the skewed sex ratio suggests a segregation of sexes during the reproductive period. Female: male ratios were more divergent for commercial gears during the months of November–May than October, June, and July (Table 1).

Males and females were first mature at 600–640 mmFL as defined by the size at which individuals exhibit developing and mature gonads from gross visual inspection (Nielsen & Johnson 1983). All black drum >640 mm were mature. All fish <590 mm were immature, but sample size during spawning season was small (n=18 females and 11 males at 460–590 mm).

Table 1

Chi-square contingency analysis of black drum *Pogonias cromis* sex ratios for commercial gears represented by a minimum of 20 individuals.

	Observed			Female:Male ratio
Gear	Male	Female	Total	
Nov, Dec, Feb, Mar, Apr, May (χ^2=79.5, df 2, p<0.001)				
Gillnet	42	105	147	1:0.4
Haul-seine	39	65	104	1:0.6
Trawl	267	126	393	0.47:1
Total	348	296	644	
Oct, June, July (χ^2 =1.18, df 2, 0.9<p<0.5)				
Gillnet	27	42	69	1:0.64
Haul-seine	27	31	58	1:0.87
Purse-seine	13	12	25	0.92:1
Total	67	85	152	

Seasonal oocyte development

Ovaries were characterized by dominance of a single population of primary growth (PG) oocytes year-round, with subsequent appearance of more advanced vitellogenic oocytes during the reproductive season. Cortical alveolar (CA)-stage oocytes, signaling onset of development, were first observed in October 1986 (Fig. 1). By November, CA and vitellogenic (V) stages were common among females and comprised 4.6 and 3.9%, respectively, of the ova counted. We noted increasing proportions of CA and V oocytes relative to counts of PG oocytes by December (Fig. 1). Cortical alveolar-stage oocytes peaked during December, and vitellogenic oocytes lagged in time, exhibiting a peak in March (Fig. 1).

We noted evidence for onset of spawning in 2 females displaying yolk coalescence of vitellogenic oocytes during November 1986. We found conclusive evidence of active spawning on 16 February 1987, when we detected hydrated oocytes (H) and postovulatory follicles (POF). No fish were caught during January 1987 due to bad weather, and there was no evidence of active spawning (i.e., atresia or postovulatory follicles) from samples examined from November, December, or early February (n=61 females). Based on the number of females containing hydrated eggs, spawning peaked in February and March (Fig. 1). Although hydrated oocytes were not detected in April (Fig. 1), presence of postovulatory follicles indicated some spawning was still occurring (Table 2). Coalescence of vitellogenic oocytes, preceding hydration and ovulation, was detected in one female sampled 12 May 1987 (Table 2).

We observed a low proportion of atretic yolked oocytes among females during the development phase prior to onset of spawning. These were similar in appearance to atretic oocytes classified by Hunter & Macewicz (1985) as alpha-stage atresia. A low incidence of atretic yolked oocytes is considered normal during ovarian development in teleosts (DeVlaming 1983). However, we noted an increase in the presence of atretic material as the reproductive season progressed. By 24 April, 13 out of 16 sampled females were classified as atretic state 1, with atretic oocytes <50% of yolked oocytes present. We noted incidence of atretic oocytes >50% of the total yolked oocytes from individuals sampled 12 May 1987, probably signaling a decline in spawning (atretic state 2). By this date, all yolked oocytes were undergoing atresia in 12 out of 22 females examined histologically, and all 22 females exhibited some atretic yolked oocytes. By 12 June, atresia of yolked oocytes was complete for all females examined (n=19), and only gonadotropin-independent PG oocytes remained (atretic state 3).

Table 2

Number of female black drum *Pogonias cromis* in reproductive condition based on histological staging for determination of spawning frequency. Day-0 designated females were actively spawning or close to onset of spawning. Day-1 designated females have been sampled at least 6 h after spawning (see Fig. 3).

Date	Day-0 spawning females	Day-1 spawning females	Total mature females*
11/11/86	2		23
12/16/86	5		23
02/03/87	9		15
02/16/87	19		22
02/20/87	18	5	20
02/24/87			2
02/27/87	6	6	12
03/06/87		4	4
03/23/87	13	12	16
03/27/87	4	10	10
04/06/87		1	8
04/24/87	3	2	16
05/12/87	1		22
Total	80	40	193
Proportion of total	0.415	0.207	
Average proportion of total	0.311		

*Total observed histologically with vitellogenic oocytes

The gonosomatic index (GSI), which is gonad weight expressed as a fraction of body weight, is a common measure of gonad development used to document seasonal changes (Nielson & Johnson 1983). We observed a marked peak in GSI for both males and females in March (Fig. 2). Females exhibited the most dramatic change in gonad weight as the season progressed, with mean gonad weight increasing to >8% of eviscerated body weight. Both sexes followed a similar pattern with respect to time of onset, peak, and decline of GSI (Fig. 2). The gonosomatic index corresponded well with histological observations (Figs. 1, 2). Females exhibited an increase in GSI above "resting" levels in November, when CA and V oocytes were present. Monthly peaks in GSI during February and March resulted from the presence of hydrated oocytes and an increase in the proportion of vitellogenic eggs. Increased atresia of yolked oocytes observed histologically in April and May, associated with decreased spawning, produced a decrease in GSI (Fig. 2). In June, when all yolked oocytes were atretic, female GSI had dropped to 0.87,

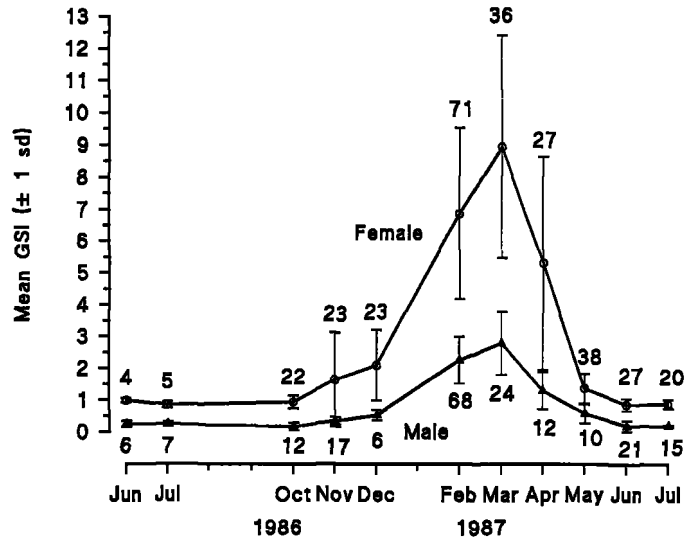

Figure 2
Mean value for gonosomatic index (GSI) for adult black drum *Pogonias cromis* (±1 SD). Sample sizes are indicated by numbers on graph.

and female GSI reached the observed minimum value of 0.84 by July (Fig. 2).

Spawning frequency

In order to estimate proximity to time of spawning and designate females as day-0 and day-1 spawners for spawning frequency calculation (Table 2), we constructed a time-scale of coalescence-stage oocytes, hydrated oocytes, and postovulatory follicles based on literature reports and our observations (Fig. 3). From previous work on related sciaenids, it is known that lipid coalescence, germinal vesicle migration, and yolk coalescence occur beginning in morning samples with hydration becoming evident as the day progresses (DeMartini & Fountain 1981, Fitzhugh et al. 1988, Brown-Peterson et al. 1988). Although exact capture times for some black drum were not known, females exhibiting germinal vesicle migration and yolk coalescence were commonly taken in haul-seine and gillnet sets which were typically landed during morning hours.

A follicle, comprised of an inner layer of epithelial granulosa cells and an outer layer of thecal cells, surrounds each hydrated oocyte. Following ovulation, POFs were present as the evacuated follicle remaining in the ovary. Recent POFs were denoted by linear arrangement of the granulosa cell layer and apical location of very prominent nuclei. These cellular arrangements imparted the appearance of a well-defined lumen and convoluted shape to the POF and were observed from ovaries sampled between 2400 and 0300 h from preliminary samples taken by hook-and-line in March 1986. We concluded that spawning occurred earlier that same night, and used these March 1986 samples as an example of recent POFs. Three females sampled from trawl landings in 1987 with recent POFs also had fully-hydrated eggs in the lumen of their ovaries, indicating active spawning and coinciding with reports of onset of spawning after dusk (Mok & Gilmore 1983, Holt et al. 1985). From interviews of commercial fishermen, capture of black drum in trawls often occurred after dusk and throughout the night, with fish being placed into ice as they were captured. We routinely sampled black drum the morning following their capture, and therefore it is likely that the recent POFs we observed are from fish captured up to 8 h after spawning (Fig. 3).

Over the 1986–87 spawning season, we sampled limited numbers of females bearing POFs (50 females taken from 8 different samples) indicating that duration of POFs may be brief. Hydration-stage oocytes, occurring together with visibly-degenerated POFs, were evident in only 19 females. Additionally, only 1 female contained recent POFs as well as degenerating POFs. Older degenerating POFs were similar in appearance to 24 h-old follicles illustrated in Hunter et al. (1986) from skipjack tuna *Katsuwonus pelamis* spawning at 23–24°C. Therefore, POF duration may be limited to 24–48 h following ovulation (Fig. 3).

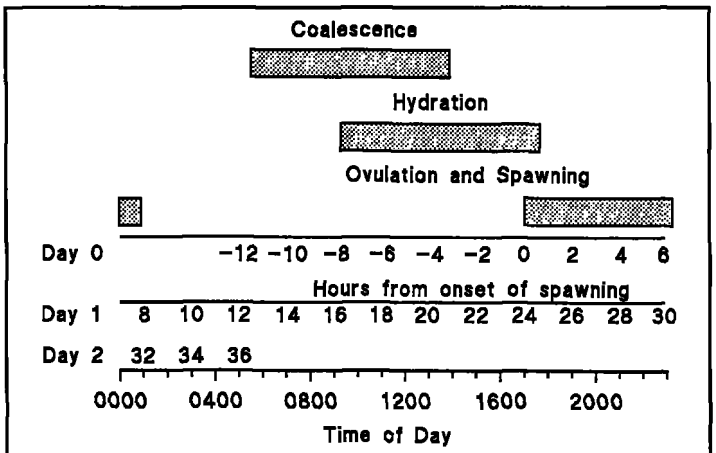

Figure 3
Generalized time-scale of final oocyte maturation and spawning of black drum *Pogonias cromis*, determined from observations and literature reports (see text).

We estimated spawning frequency by examining ovarian tissues of 193 mature females (vitellogenic oocytes present) sampled over the spawning season. We define spawning season as the period during which spawning condition was histologically evident, from first evidence of coalescence of vitellogenic oocytes on 11 November 1986, until atresia of vitellogenic oocytes was occurring in all females encountered on 12 May 1987 (Table 2). The numbers of day-0 and day-1 spawning females was 80 and 40 (frequencies = 0.415 and 0.207) for this period, respectively. This resulted in an overall seasonal frequency of 0.311, or each female spawning on average once every 3 d (Table 2). From November 1986 through May 1987, 50 of 193 females (26%) contained POFs. This method of estimating spawning frequency would correspond to a spawning frequency of once every 4 d, or a total of 46 times, during the spawning season.

Batch fecundity

We determined batch fecundity for 25 visibly-hydrated females which possessed no recent POF in histological sections that would indicate egg shedding. The range in batch fecundity was 7.4×10^5 hydrated oocytes for a 4.3 kg female, to 3.8×10^6 hydrated oocytes for a 4.8 kg female, indicating wide variation in fecundity based on body size (Fig. 4). The number of hydrated oocytes/g of ovary weight ranged from 1046 to 4902. Based on eviscerated body weight, the number of eggs/g ranged from 131 to 793. The mean value for batch fecundity was 1.6×10^6 for a mean eviscerated weight of 6.1 kg.

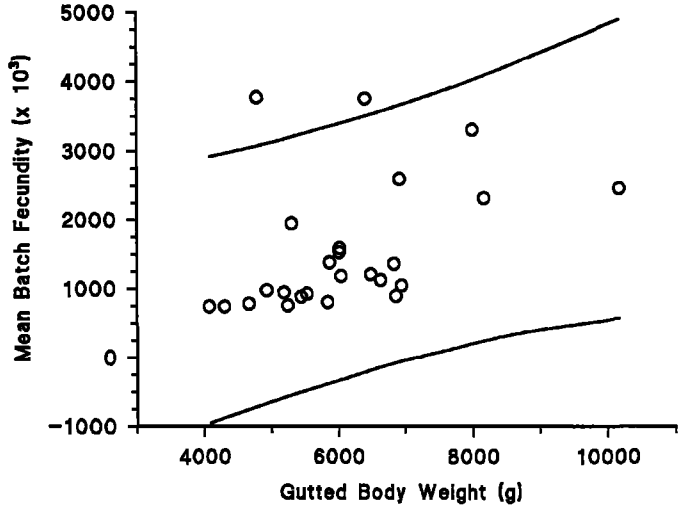

Figure 4
Batch fecundity and eviscerated body weight with 95% confidence interval for hydrated female black drum *Pogonias cromis*, sampled in February and March 1987.

Location of tissue samples

Black drum possess relatively large gonads for teleosts, and we sampled ovaries weighing 0.4–1.6 kg laden with hydrated oocytes. No significant differences were detected between positions within a lobe or between right and left ovarian lobes for number of hydrated oocytes/g of ovarian tissue (Table 3). However, counts of hydrated oocytes/g were lower for the anterior position ($\bar{x}$ 1780) than for either mid- or posterior ovarian regions ($\bar{x}$ 2013 and 1928, respectively) (Table 3).

Discussion

We noted differences in sex ratios between samples collected by various fishing gears during the period of reproductive development and spawning, November–May. Landings by offshore trawlers (where spawning females were found in February and March) were clearly dominated by males. Females dominated in inshore samples from all gears (primarily gillnet and haul-seine landings), but this female dominance was not as prevalent outside the breeding season during October, June, and July. These divergent ratios suggest sexes are spatially segregated for periods during the reproductive season. This difference in sex ratios has been noted in other fisheries where a higher proportion of males attend those females in active spawning condition on the spawning grounds (DeMartini & Fountain 1981, Hunter & Goldberg 1980).

In a synthesis of previous studies, Simmons & Breuer (1962) reported age-at-maturity for black drum to be 2 yr at 320 mm based on scale increments, length frequencies, and gross assessment of ripe females (granular roe observed) in Texas waters. Pearson (1929) found drum as small as 270 mm with developing ovaries. Murphy & Taylor (1989) provide evidence for larger sizes-at-maturity, with males maturing at 590 mm (4–5 yr old) and females maturing at 650 mm (5–6 yr old). Our findings of age-at-maturity agree with Murphy & Taylor's (1989) estimates. Mature females and males occurred at a size-range of 600–640 mmFL, corresponding to ages 3–8 yr (Beckman et al. 1990). A mature female with hydrated eggs was observed as small as 625 mmFL; this indicates that size- or age-at-maturity for northern Gulf of Mexico stocks is greater than previously estimated by Simmons & Breuer

Table 3

Effect of location of tissue samples of black drum *Pogonias cromis* for hydrated oocyte counts per unit of ovary weight (g). Locations are anterior (i), mid (ii), and posterior (iii) of ovarian lobes.

	Mean, SE of oocytes/g, and number of tissue samples								
	Right lobe			Left lobe			Both lobes		
Locations	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n
i	1714	91	25	1846	170	25	1780	96	50
ii	2025	245	25	2000	199	25	2013	156	50
iii	1944	149	25	1911	180	25	1928	116	50
Total	1895	100	75	1919	105	75			

Two-way ANOVA:

Source of variance	df	SS	MS	F	PR>F
Lobe	1	22490	22490	0.03	0.87
Segment	2	1385533	692767	0.87	0.42
Interaction	2	213348	106674	0.13	0.87
Error	144	14701071	796535		
Total	149	116322441			

(1962) and Pearson (1929) for black drum from Texas waters.

Multiple oocyte stages were present throughout the 1986–87 spawning season, including primary growth (PG), cortical alveolar (CA), and vitellogenic (V) stages. Primary-growth oocytes were present year-round and are a gonadotropin-independent stage (Wallace & Selman 1981, DeVlaming 1983). Oocyte recruitment from this PG population and onset of seasonal oogenesis was signaled by the appearance of CA oocytes in October. Vitellogenic oocytes were noted in November, and both CA and V oocytes persisted until May, indicating the potential for a protracted spawning season.

Descriptions of the breeding season for black drum are varied. Gonad development and possible spawning have been reported during the summer (Pearson 1929, Cornelius 1984 cited in Cody et al. 1985). Our June, July, and October samples did not indicate that spawning was evident. By November, reproductive development for two females (yolk coalescence and final oocyte maturation in histological sections) indicated the potential for spawning to occur. Capture of black drum larvae from offshore Louisiana waters has been reported as early as December (Ditty 1986). Pearson (1929) reported the primary spawning season was February to May. Cody et al. (1985) described seasonality of gonad development of black drum in Texas and reported gravid females during November–April, with spawning or spent stages predominant during February–April. From Florida, Murphy & Taylor (1989) and Peters & McMichael (1990) also report the reproductive season ranges from November to April with February–March spawning peaks.

All the changes noted with the onset, peak, and decline of the spawning season were reflected both in histological samples of ovaries and in gonad weight changes relative to body weight (GSI) for females. Increase in proportion of vitellogenic oocytes was associated with GSI increase in November and December. Appearance of hydrated oocytes and postovulatory follicles in February and March coincided with highest values for GSI. Subsequent appearance of atretic vitellogenic oocytes in April, and increase in atresia in May and June, were associated with declines in gonad weights reflected by decreasing GSI. The GSI seasonal pattern for males coincided with the pattern for females, and suggests a synchrony in development of reproductive states for both sexes. However, mean GSI values must be interpreted with caution. For the same stage of oocyte development, a larger individual may exhibit proportionally larger ovaries and a greater GSI value than a smaller individual (DeVlaming et al. 1982). We apply the GSI here only as a relative measure of changes in reproductive condition over the spawning season, and not as a specific measure of reproductive readiness or histological stage.

Black drum spawn in inside (estuarine, bay) as well as in outside (coastal waters seaward of inlets) waters. Pearson (1929) indicated spawning took place in Gulf waters off Texas, although Simmons & Breuer (1962) presented evidence for spawning in estuaries. Osburn & Matlock (1984) present evidence from tagging studies for a "quasi-permanent" movement of black drum >4 yr from bays to the Gulf, where they may act as spawning stock. Jannke (1971) cited evidence of estuarine spawning in the Florida Everglades, but also indicated that spawning occurred outside the estuarine portion of the park. Peters & McMichael (1990) report that spawning in the Tampa Bay region was likely to have occurred both inside and outside the bay. We also noted spawning activity over a gradient from offshore to inshore. Examination of black drum in hydrated condition from trawl landings during February and March indicated spawning was occurring in coastal waters off Louisiana. During late March, however, females in hydrated condition were taken by haul-seine from inshore estuarine waters east of the Mis-

sissippi River. Drumming behavior associated with spawning was noted in Caminada Pass, Louisiana in April, further documenting inshore reproductive activity (Donald Baltz, Coastal Fish. Inst., LA State Univ., Baton Rouge, pers. commun.).

The dynamic of changing spawning locations may have a seasonal component related to water temperature. Mok & Gilmore (1983) analyzed sound production from black drum in Florida waters and noted "loud drumming," which they associated with spawning, occurring at 18–20°C. They also noted cessation of this drumming during a temperature drop to 13–15°C. Peters & McMichael (1990) provided more direct evidence for onset of spawning at 16–20°C. By correlating seasonal water temperature with larval birthdates, peak births were calculated to have occurred in March when temperatures reached 21–24°C. Although we did not have precise locations and temperatures for commercial catches, our samples of hydrated-oocyte and POF-bearing females indicate that spawning may have predominated in outside waters in February (e.g., trawl landings) and moved to inside waters as seasonal temperatures increased (haul-seine and gillnet landings in March and April). Other factors not examined may influence spawning, including moon phase and tidal period (Peters & McMichael 1990).

Postovulatory follicles probably last longer than 24 h at sea temperatures encountered in coastal Louisiana waters in February and March (19–22°C). Hunter & Macewicz (1985) found POFs for 3–4 d from northern and peruvian anchovies (*Engraulis mordax* and *E. ringens*) spawning at 13–19°C. Based on a higher spawning temperature of 23–24°C, Hunter et al. (1986) found 24 h-old follicles in skipjack tuna that appeared similar to those in northern anchovy held 48 h. Our day-1 POFs appeared similar to 24 h POFs for skipjack tuna shown in Hunter et al. (1986). We estimated black drum follicle duration to be at least 32 h old, due to the presence of recent POFs and older-degenerating POFs together in the same histological sections (i.e., 0–8 h plus 24 h, respectively) which is consistent with spawning on successive nights. If follicles are identifiable well past 24 h, our estimate of average duration between spawning would increase.

Our estimates of spawning frequency, once every 3 or 4 d, are similar to other sciaenid species. Tucker & Faulkner (1987) report a daily spawning fraction of 0.35 (once every 3 d) for captive spotted seatrout. Brown-Peterson et al. (1988) calculated an average daily percentage of wild seatrout in ripe condition to be 27.5% (indicating spawning once every 3.6 d) over a 6 mo reproductive season. Red drum have displayed a spawning fraction of 0.68 (once every 1.5 d) in captivity over a 76 d period (Arnold et al. 1977).

The pattern of appearance of vitellogenic oocytes supports our contention that oocyte recruitment continued during the reproductive season. Therefore, the yolked-oocyte population was not deterministic or representative of annual fecundity (Hunter et al. 1985). Of females examined histologically in February, 73% showed evidence of recent spawning (day-0 females), yet the proportion of vitellogenic oocytes from females did not reach a maximum until March. In contrast, a species with a determinant oocyte development pattern could exhibit multiple spawns but the proportion of vitellogenic oocytes would decrease following onset of spawning (Hunter et al. 1985). With continuous recruitment of batches of oocytes, the traditional method to determine fecundity by enumerating vitellogenic oocytes prior to onset of reproduction (e.g., Bagenal 1968) would underestimate potential fecundity. This method necessitates counting of hydrated eggs just prior to ovulation, i.e., determining batch fecundity and number of spawns in the season (Hunter et al. 1985).

Previously, little fecundity information has been reported for black drum (Sutter et al. 1986). Pearson (1929) estimated fecundity at 6 million eggs for one 110 cm gravid female (107cmFL, 16.4 kg eviscerated weight)* based on extrapolation of wet weight for 60 eggs. Our computation of batch fecundity was 1.6 million eggs for a 6.1 kg female (mean eviscerated weight of 25 females). Figure 4 and comparison with Pearson's result suggest that batch fecundity is a function of body size, but we found this relationship to be quite variable (Fig. 4). While these data do not appear to fit a linear relationship as closely as for smaller sciaenids (DeMartini & Fountain 1981, Brown-Peterson et al. 1988), we only sampled hydrated females measuring 660–876 mmFL. Because females >1000 mm are occasionally landed (e.g., Beckman et al. 1990), a broader range of sizes could illuminate the functional relationship between size and fecundity. Batch size may vary also with the reproductive period and may be higher earlier in the spawning season. Our sample size was too small to detect changes in batch fecundity over the breeding season. However, the pattern of vitellogenesis and GSI provides evidence that spawning peaked in March. The proportion of females in spawning condition was also highest in March. Conover (1985) demonstrated a quadratic batch-fecundity relationship for Atlantic silversides during the breeding season. He postulated that this pattern may occur when optimal

* Calculated from TL-FL regression reported in Murphy & Taylor (1989). The relationship between eviscerated body weight (BW) and fork length (FL) is given by the equation: Ln BW = 2.8835 Ln FL - 10.382 (n=100, r^2=0.964, range 459-1122 mmFL).

conditions for reproduction exist at about the same time each year.

The batch fecundity estimate multiplied by the frequency of spawning provides an estimate of annual fecundity (Hunter & Macewicz 1985, Hunter et al. 1985). For example, annual production could be as high as 32 million eggs for a 6.1kg female with an average clutch of 1.6 million eggs over 20 spawns (assuming spawning every 3 d on average during February and March). Although this estimate of annual fecundity is high for wild fish, spawning patterns in captivity for a closely-related sciaenid, red drum *Sciaenops ocellatus*, corroborates this magnitude of egg production. Three captive female red drum produced 6×10^7 eggs over 76 d, or roughly 20 million eggs/female (Arnold et al. 1977).

Although we found no significant differences in hydrated egg counts between ovarian lobes or among locations within a lobe, we observed the maximum number of hydrated oocytes in the mid-region of ovaries. Hydrated eggs per unit of ovary weight were lowest for the anterior region of the ovary, and may have been due to decreased vascularization or the hydration rate (Hunter et al. 1985, Fitzhugh et al. 1988). In future sampling, we recommend multiple samples be taken for accurate batch-fecundity determinations due to the large ovary size and potential for heterogeneity of hydrated oocytes among locations within the ovary.

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Citations

Arnold, C. R., W. H. Bailey, J. L. Lasswell, T. D. Williams, & A. Johnson
1977 Laboratory spawning and larval rearing of red drum and southern flounder. Proc., Annu. Conf. Southeast Assoc. Fish Wildl. Agencies 31:347–440.

Bagenal, T. B.
1968 Fecundity. *In* Ricker, W.E. (ed.), Methods for assessment of fish production in freshwaters, p. 160–169. IBP (Int. Biol. Prog.) Handb. 3.

Beckman, D. W., A. L. Stanley, J. H. Render, & C. A. Wilson
1990 Age and growth of black drum in Louisiana waters of the Gulf of Mexico. Trans. Am. Fish. Soc. 119:537–544.

Brown-Peterson, N., P. Thomas, & C. R. Arnold
1988 Reproductive biology of the spotted seatrout, *Cynoscion nebulosus*, in South Texas. Fish. Bull., U.S. 86:373–388.

Cody, T. J., K. W. Rice, & C. E. Bryan
1985 Distribution and gonadal development of black drum in Texas gulf waters. Manage. Data Ser. 72, Tex. Parks Wildl. Dep., Coast. Fish. Branch, 16 p.

Conover, D. O.
1985 Field and laboratory assessment of patterns in fecundity of a multiple spawning fish: The Atlantic silverside *Menidia menidia*. Fish. Bull., U.S. 83:331–341.

Cornelius, S. E.
1984 Contribution to the life history of black drum and analysis of the commercial fishery of Baffin Bay, Vol. II. Tech. Bull. 6, Caesar Kleberg Wildl. Res. Inst., Tex. A&I Univ., Kingsville, 53 p.

DeMartini, E. E., & R. K. Fountain
1981 Ovarian cycling frequency and batch fecundity in the Queenfish, *Seriphus politus*: Attributes representative of serial spawning fishes. Fish. Bull., U.S. 79:547–559.

DeVlaming, V.
1983 Oocyte development patterns and hormonal involvements among teleosts. *In* Rankin, J.C., et al. (eds.), Control processes in fish physiology, p. 176–199. John Wiley, NY.

DeVlaming, V., G. Grossman, & F. Chapman
1982 On the use of the gonosomatic index. Comp. Biochem. Physiol. 73A:31–39.

Ditty, J. G.
1986 Icthyoplankton in neritic waters of the Northern Gulf of Mexico off Louisiana: Composition, relative abundance, and seasonality. Fish. Bull.,U.S. 84:935–946.

Fitzhugh, G. R., T. G. Snider, & B. A. Thompson
1988 Measurement of ovarian development in red drum (*Sciaenops ocellatus*) from offshore stocks. Contrib. Mar. Sci., Suppl. to vol. 30:79–86.

Hildebrand, S. F., & W. C. Schroeder
1928 Fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43(1), 388 p.

Holdway, D. A., & F. W. H. Beamish
1985 The effect of growth rate, size, and season on oocyte development and maturity of Atlantic cod (*Gadus morhua* L.). J. Exp. Mar. Biol. Ecol. 85:3–19.

Holt, G. J., S. A. Holt, & C. R. Arnold
1985 Diel periodicity of spawning in Sciaenids. Mar. Ecol. Prog. Ser. 27:1–7.

Htun-Han, M.
1978 The reproductive biology of the dab *Limanda limanda* (L.) in the North Sea: Seasonal changes in the ovary. J. Fish Biol. 13:351–359.

Hunter, J. R., & S. R. Goldberg
1980 Spawning incidence and batch fecundity in Northern Anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641–652.

Hunter, J. R., & B. J. Macewicz
1985 Measurement of spawning frequency in multiple spawning fishes. *In* Lasker, R.L. (ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*, p. 79–94. NOAA Tech. Rep. NMFS 36.

Hunter, J. R., N. C. H. Lo, & R. J. H. Leong
1985 Batch fecundity in multiple spawning fishes. *In* Lasker, R.M. (ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*, p. 67–77. NOAA Tech. Rep. NMFS 36.

Hunter, J. R., B. J. Macewicz, & J. R. Sibert
1986 The spawning frequency of Skipjack Tuna, *Katsuwonus pelamis*, from the South Pacific. Fish. Bull.,U.S. 84(4):895–903.

Jannke, T. E.
1971 Abundance of young sciaenid fishes in Everglades National Park, Florida, in relation to season and other variables. Sea Grant Tech. Bull. 11, Univ. Miami Sea Grant Prog., Miami.

Mok, H. K., & R. G. Gilmore
1983 Analysis of sound production in estuarine aggregations of *Pogonias cromis*, *Bardiella chrysoura*, and *Cynoscion nebulosus* (Sciaenidae). Bull. Inst. Zool., Acad. Sin. (Taipei) 22:157–186.

Murphy, M. D., & R. G. Taylor
1989 Reproduction and growth of black drum, *Pogonius cromis*, in northeast Florida. Northeast Gulf Sci. 10(2):127–137.

Nielson, L. A., & D. L. Johnson (editors)
1983 Fisheries techniques. Am. Fish. Soc., Bethesda, 468 p.

NMFS (National Marine Fisheries Service)
1986 Final secretarial Fishery Management Plan, regulatory impact review, initial regulatory flexibility analysis, and final EIS for the red drum fishery of the Gulf of Mexico. Natl. Mar. Fish. Serv., NOAA, Southeast Region, St. Petersburg FL 33702, Dec. 1986.

Osburn, H. R., & G. C. Matlock
1984 Black drum movement in Texas bays. N. Am. J. Fish. Manage. 4:523–530.

Pearson, J. C.
1929 Natural history and conservation of the redfish and the commercial sciaenids on the Texas Coast. Fish. Bull., U.S. 44:129–214.

Peters, K. M., & R. H. McMichael Jr.
1990 Early life history of the black drum *Pogonias cromis* (Pisces:Sciaenidae) in Tampa Bay, Florida. Northeast Gulf Sci. 11(1):39–58.

SAS
1985 SAS user's guide: Statistics. Version 5 ed. SAS Inst. Inc., Cary NC, 956 p.

Selman, K., & R. A. Wallace
1986 Gametogenesis in *Fundulus heteroclitus*. Am. Zool. 26:173–192.

Simmons, E. G., & J. P. Breuer
1962 A study of redfish, *Sciaenops ocellata* Linnaeus, and black drum *Pogonias cromis* Linnaeus. Publ. Inst. Mar. Sci. Univ. Tex. 8:184–211.

Sutter, F. C., R. S. Waller, & T. D. McIlwain
1986 Species profiles: life histories and environmental requirements of coastal fisheries and invertebrates (Gulf of Mexico)-black drum. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.51), U.S. Army Corps of Eng. TR EL-82-4, 10 p.

Tucker, J. W., & B. E. Faulkner
1987 Voluntary spawning patterns of captive spotted seatrout. Northeast Gulf Sci. (1):59–63.

Wallace, R. A., & K. Selman
1981 Cellular and dynamic aspects of oocyte growth in teleosts. Am. Zool. 21:325–343.

Ware, D. M.
1982 Power and the evolutionary fitness of teleosts. Can. J. Fish. Aquat. Sci. 39:1–13.