A review of age, growth, and reproduction of cobia *Rachycentron canadum*, from US water of the Gulf of Mexico and Atlantic ocean

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A Review of Age, Growth, and Reproduction of Cobia, *Rachycentron canadum*, from U.S. Waters of the Gulf of Mexico and Atlantic Ocean

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ABSTRACT

A review of available scientific information on the age, growth, and reproduction of cobia, *Rachycentron canadum*, from United States waters of the Gulf of Mexico and Atlantic Ocean is provided. Periodicity of annulus formation on sectioned sagittae has been partially validated by marginal-increment analysis, and age in years is estimated as the number of observed opaque bands. Growth in length for both sexes is rapid through age 2. Females grow faster and live longer than males and dominate all age groups. Gulf males reached age 9 and 1,390 mm FL; females reached age 11and 1,651 mm FL. Atlantic males reached age 14 and 1,360 mm FL; females reached age13 and 1,420 mm FL. Estimates of the von Bertalanffy growth parameters (L_∞, K, and t_0) within studies showed significant differences in L_∞ and K for the sexes, whereas estimates for t_0 were not always significantly different. Ages 2 - 5 dominated the age structure of Gulf and Atlantic samples. Cobia were fully recruited to the northeastern Gulf recreational fishery at age 4, and the instantaneous rate of total mortality (Z) estimated for fully recruited cobia ages 4 - 8 was 0.75. Cobia have an extended spawning season throughout their range in United States waters, averaging five months (mid-April-August) in the Atlantic Ocean and six months (April-September) in the Gulf of Mexico. Some Gulf females appear to cease spawning by July. Female cobia can obtain sexual maturity as small as 700 mm FL. Histological analysis shows cobia are a multiple spawning species; females are estimated to spawn once every five days throughout most of the U.S. region. Batch fecundity increases significantly with FL and ovary-free body weight (OFBW); mean relative batch fecundity is 53.1 ± 9.4 eggs/g OFBW. While the testis of males contain sperm year-round, spermatogenesis only takes place from February - August, and spermatogonial proliferation is observed during non-spawning months.

KEY WORDS: *Rachycentron canadum*, age, growth, reproduction

INTRODUCTION

Cobia, *Rachycentron canadum*, are large, coastal pelagic fish of the monotypic family Rachycentridae and are distributed worldwide in tropical and subtropical seas, except for the eastern Pacific (Shaffer and Nakamura 1989). In the western Atlantic Ocean, cobia occur from Massachusetts and Bermuda to Argentina (Briggs 1960) but are most common along the United States (U. S.) Atlantic coast and in the northern Gulf of Mexico (Shaffer and Nakamura, 1989). In the Gulf of Mexico, cobia range from Key West, Florida and along the entire coast to Campeche, Mexico (Dawson 1971). In this paper, reference will be made to the U.S. Gulf of Mexico and Atlantic Ocean as Gulf and Atlantic, respectively.

Cobia are migratory fish, and in the eastern Gulf cobia typically migrate from their wintering grounds off south Florida into northeastern Gulf waters during early spring. Cobia occur off northwest Florida, Alabama, Mississippi and southeast Louisiana from late-March through October and return to the wintering grounds in the fall (Franks et al. 1999, Biesiot et al. 1994). However, Howse et al. (1992) reported that some cobia over-winter in the northern Gulf at depths of 100 - 125 m. Cobia move along the U.S. east coast as far north as the Chesapeake Bay during summer, then presumably migrate to south Florida, although it is unclear where cobia from the U.S. Atlantic overwinter (Smith 1995). Timing of the migrations appears related to spawning and possibly to the availability of important prey species.

Cobia is a highly-prized recreational species in the Gulf and Atlantic and is caught incidentally in several commercial fisheries (Shaffer and Nakamura 1989). Recreational and commercial regulations for cobia in U. S. waters consist of a minimum size of 838 mm fork length (33 inches) and daily bag and possession limits of 2 fish per person (GM&SAFM, 1990). The cobia catch (commercial and recreational) from the Gulf and Atlantic, combined, averaged 1 million kg per year during a recent 14 - year period (1984-97, Scott and Phares, 1999). The recreational catch averaged ~90 % of the total harvest for the 14-year period, and the majority (~70%) of that catch came from the Gulf with an average of 0.63 million kg per year (Scott and Phares 1999).

At the present time, there are not enough data to determine the status of the cobia fishery. The Gulf of Mexico Fishery Management Council is in the process of conducting an assessment of the cobia stock in the Gulf waters. An MSY of 2.2 million pounds (1 million kg; Gulf and Atlantic, combined) currently is substituted in the preliminary assessments in place of unavailable information on the spawning potential ratio (SPR, Scott and Phares 1999). More information on harvest levels, SPR, bycatch, and recruitment are needed to better assess the stocks.

The purpose of this paper is to provide a review of current information on age, growth, and reproductive biology of cobia from waters of the United States. We intend that our present contribution build upon and supplement the FAO cobia synopsis published by Shaffer and Nakamura (1989). All references for this review reported on cobia sampled primarily from the recreational fishery. Readers are advised to consult the primary sources for information on methods and detailed descriptions of each study.

SIZE, AGE, AND GROWTH OF COBIA

Size Composition

Even though most specimens were sampled from the recreational fishery, most authors believed their samples were not biased towards larger fish, since samples typically consisted of a large number of fish representing a broad size range.

Table 1 summarizes the weight and length ranges reported by the various studies. Cobia from the Gulf tended to be larger than those from the Atlantic, although the minimum size of males and females were similar in most studies.

Table 1. Size range and mean size of cobia, *Rachycentron canadum*, sampled in U.S. Gulf of Mexico and south Atlantic studies.

			Length (FL, mm)		Weight (TW, kg)		
Area	**Sex**	***n***	**Range**	**Mean**	**Range**	**Mean**	**Reference**
Virginia	M	155	- -1194	–	- -19.0	–	Richards
	F	98	- -1377	–	- -34.0	–	(1967)[2]
North	M	174	390 -1360	–	0.5-32.0	–	Smith
Carolina	F	182	440 -1420	–	0.7-32.2	–	(1995)[1]
Carolinas	M	28	801 -1,130	950.7	5.9 - 9.8	11.40	Burns et al.
	F	45	941 -1,380	1,155.7	10.0-34.9	20.47	(1998)[1]
FL Atlantic	M	28	830 -1,130	960.0	5.8-20.9	11.53	"
	F	55	830 -1,290	1,000.8	6.8-25.9	12.79	
FL Keys	M	20	701 -1,000	86.2	3.9 - 8.2	6.67	"
	F	28	700 -1,060	86.0	3.2-19.5	7.98	
FL Gulf	M	41	361 -1,220	760.6	0.2-26.3	6.72	"
	F	75	351 -1,270	820.3	0.8-25.4	9.16	
Northeastern	M	66	380 -1,390	970.3	0.3- 4.4	10.01	"
Gulf	F	216	370 -1,631	1,050.4	0.3- 8.4	15.45	
Northeastern	M	275	345 -1,450	952.0	0.3-29.0	10.5	Franks et al.
Gulf	F	730	335 -1,651	1,050.0	0.3-62.2	16.6	(1999)
Western	M	464	528 -1,432	–	1.5-30.8	–	Thompson
Louisiana	F	218	358 -1,445	–	1.0-45.6	–	et al. (1992)
Texas	M	20	310 -1,050	950.8	–	–	Burns et al.
	F	61	311 -1,280	950.8			(1998)[1]

[1] FL lengths originally reported in centimeters, converted to millimeters
[2] FL reported in inches (converted to mm), TW reported in pounds (converted to kg)
- = not reported

Size Relationships

Regressions to predict FL from TL and TL from FL are shown in Table 2. Relationships were calculated using the linear regression models: FL = a + bTL and TL = a + bFL. The slopes of the regressions did not differ significantly between males and females for any study, and all reported $r^2 \geq 0.95$.

Length-weight relationships between males and females did not differ significantly for any of the studies, although females were typically larger than males. Length-weight regressions, using log-transformed (base 10) data, were calculated to predict TW from FL (Table 2). While all regressions were statistically significant, the strength of the relationship varied from $r^2 = 0.51$ for female cobia in the Carolinas (Burns et al., 1998) to $r^2 = 0.98$ for sexes combined in North Carolina (Smith, 1995).

Annulus Formation

Richards (1967) used scales to age cobia, whereas Thompson et al. (1992), Smith (1995), Burns et al. (1998), and Franks et al. (1999) aged cobia based on analysis of transverse-sectioned sagittal otoliths. Based on marginal increment analysis, cobia appear to form a single annulus on sagittae each year during spring - summer (Thompson et al. 1992, Smith 1995, Burns et al. 1998, Franks et al. 1999). Thus, age in years for cobia is presumed equal to the number of opaque bands observed in sectioned sagittae. Although the periodicity of annulus formation on otoliths coincides with the cobia spawning season in the northern Gulf (Burns, et al. 1998, Brown-Peterson et al. 2001) and off the U.S. east coast (Smith 1995), annulus deposition may be more related to cobia migrations, at least in the northern Gulf in spring (Franks et al. 1999). Franks et al. (1999) reported that sagittae of several sexually mature cobia sampled in March and April (early part of the spawning season) already showed distinctive opaque bands, as did sexually immature fish in spring. Thus reproduction may not be the sole determining factor related to annulus formation; environmental and physiological factors should not be discounted.

Estimated Age

Some studies provided age-length keys for both sexes to provide estimates of the age structure of cobia from the respective U.S. regions. Richards (1967) developed age-length keys from back-calculated size-at-age data, while Burns et al. (1998) and Franks et al. (1999) used observed ages at lengths to derive age-length keys.

Typically there was a wide range of lengths within most age groups for both sexes of cobia, e.g., Franks et al. (1999) found that males within a 1,000- 1,050 mm size group ranged from ages 2 to 7 and within a 1,200 - 1,250 mm FL group ranged from ages 4 to 9. Females within a 1,350 - 1,400 mm FL group ranged from ages

5 to 9. This variation in size makes it difficult to precisely estimate the age of cobia from length alone. Franks et al. (1999) reported the largest cobia by weight in their sample weighed 62.2 kg, which was slightly greater than the all-tackle world record weight for cobia (61.5 kg) reported by the International Game Fish Association (1997). However, at a FL of 1,610 mm and age 8, this specimen was neither the longest nor the oldest in their sample. A prolonged spawning season and multiple spawns characteristic of cobia (Lotz et al., 1996; Brown-Peterson et al., 2001) probably account for the wide variation in size of young-of-the-year cobia and, in part, for other age groups as well.

Table 2. Length-length, length-weight, and otolith weight-age regressions for cobia, *Rachycentron canadum*, from U.S. waters. FL = fork length (mm), TL = total length (mm), WT = total weight (kg), OTWT = otolith weight (g), and AGE = age in years. Values in parentheses are standard errors. M = male, F = female.

			Y = a + bX			
Area	**Y**	**X**	**a**	**b**	**r^2**	**Reference**
Virginia	log_{10}WT	log_{10}FL	-3.51	3.08		Richards (1967)[1]
No. Carolina	TL	FL	-0.9	1.10	0.99	Smith (1995)[1]
No. Carolina	log_{10}WT	log_{10}FL	-13.0	3.40	0.98	"
Carolinas	"	"	(M) 0.10	2.86	0.86	Burns et al. (1998)[1]
			(F) 0.24	2.55	0.51	
Florida	"	"	(M) 0.0001	2.89	0.79	"
Atlantic			(F) 0.021	3.55	0.82	
Florida	"	"	(M) 0.006	3.42	0.90	"
Gulf			(F) 0.002	3.15	0.90	
Northeastern	"	"	(M) 0.37	3.07	0.89	"
Gulf			(F) 0.001	2.22	0.77	
Northeastern	FL	TL	9.9494	0.8916	0.98	Franks et al.
Gulf			(3.5691)	(0.0032)		(1999)
	TL	FL	1.6661	1.1088	0.98	
			(3.9964)	(0.0040)		
Northeastern	log_{10}WT	log_{10}FL	-9.2445	3.4287	0.97	"
Gulf			(0.6474)	(0.0215)		
Northeastern	Age	OTWT	(M) 0.0081	0.0072	0.78	"
Gulf			(0.0012)	(0.0003)		
			(F) 0.0006	0.0110	0.84	
			(0.0010)	(0.0003)		
Western	FL	TL	0.87	0.94	0.98	Thompson et al.
Louisiana	TL	FL	1.13	0.57	0.98	(1992)
Western	log_{10}WT	log_{10}FL	3.80	3.24	0.97	"
Louisiana						
Western	Age	OTWT	(M)0.09	0.31	0.82	"
Louisiana			(F) 0.08	0.36	0.81	

[1] Lengths originally reported in centimeters, converted to millimeters

Table 3 shows the mean observed length-at-age for male and female cobia reported by studies conducted in the U.S. Atlantic (2, Carolinas) and the Gulf of Mexico (2, NEGOM). These studies provide for a comparison of mean FL-at-age within and between the two regions and were selected because samples from the studies contained the greatest number of specimens used for age estimations among all available cobia studies. Burns et al. (1998) and Franks (1999) reported similar mean length-at-age for their respective samples of male and female cobia from the NEGOM as well as for cobia of both sexes from the Carolinas that were age 4 or less (Burns et al. 1998). However, mean length-at-age reported by Smith (1995) for male and female cobia was, with few exceptions, less than that reported by Burns et al. (1998) and Franks et al. (1999) for every comparable age class. The studies indicate that Gulf cobia reach a greater length than cobia of comparable age from the U.S. Atlantic but that Atlantic cobia live longer.

Maximum ages of cobia from Louisiana (Thompson et al. 1992; males, 10; females, 10) and Virginia (Richards 1967, 1977; males, 10; females, 9) were similar to the findings of Franks et al. (1999) (males, age 9; females, age 11) for the northeastern Gulf of Mexico (NEGOM). However, Burns et al. (1998) reported the oldest male and female cobia in their NEGOM sample as 8 and 6 years, respectively. Smith (1995) reported a maximum age of 14 for male and age 13 for female cobia from North Carolina and commented that erosion on scale edges may have caused Richards (1967) to underestimated the ages of Virginia cobia. Burns et al. (1998) reported three age-11, one age-12, and one age-13 fish from the Carolinas. Additionally, there was a slightly higher percentage of females greater than six years old from the Carolinas than for other Gulf and Atlantic regions (Burns 1998). In general, cobia off the U.S east coast appear to live longer than their Gulf counterparts. Interestingly, the results of cobia tagging programs have shown that there is a mixing of cobia between the Gulf and Atlantic (Franks et al. 2000), and yet no fish older than age 11 have been sampled in the Gulf.

All studies reported that mean observed lengths at age for females were larger than those for males for age classes 1 and greater. Additionally, longevity of male and female cobia appears to differ. Richards (1967, 1977), Thompson et al. (1992), and Franks et al. (1999) found that males older than age 7 and females older than 8 were rare. Smith (1995) sampled few males and females greater than age 10, and Burns et al. (1998) reported a general trend among all regions (Gulf and U.S. Atlantic) they sampled which showed, with the slight exception of the Carolinas, few males and females older than age 7.

Predicted age

Thompson et al. (1992) and Franks et al. (1999) reported otolith weight was significantly related to cobia age (Table 2). Franks et al. (1999) found the slopes of the otolith weight-age regressions to be significantly different for males and females ($P < 0.0001$).

Table 3. Mean observed fork length (mm) for male and female cobia, *Rachycentron canadum*, from the U.S. Gulf of Mexico and south Atlantic Ocean. M = Male, F = Female. Numbers in parentheses are ± 1SE.

Age	North Carolina[1]				Carolinas[2]				NEGOM[3]				NEGOM[4]			
(yr)	*n*	M	*n*	F	*n*	M	*n*	F	*n*	M	*n*	F	*n*	M	*n*	F
0									1	380	3	487	5	439 (30)	28	409 (6)
1	6	500 (4)	3	550 (4)	3	850			2	656	3	883	14	705 (26)	28	720 (22)
2	22	740 (2)	18	810 (3)	7	924	2	948	10	919	61	981	47	885 (9)	103	956 (8)
3	41	820 (1)	50	890 (1)			1	1130	31	984	67	1075	47	971 (10)	116	1056 (7)
4	32	880 (1)	23	1020 (2)			3	1037	10	1020	32	1166	35	1034 (14)	64	1140 (10)
5	20	920 (1)	13	1060 (1)	2	1010	6	1003	2	1065	16	1221	16	1070 (17)	31	1248 (18)
6	7	950 (2)	20	1110 (2)	6	1028	6	1119	5	1156	12	1313	1	1140	7	1346 (38)
7	6	1000 (2)	11	1170 (2)	2	1032	5	1230	1	1100			3	1198 (87)	5	1385 (44)
8	8	990 (2)	8	1230 (2)	1	985	6	1263	1	1025					8	1553 (27)
9	6	1070 (6)	7	1250 (2)	1	1050	6	1199					2	1250 (10)	3	1507 (70)
10	5	1050 (1)	3	1270 (5)											1	1613
11	6	1050 (2)					3	1357							1	1568
12			3	1270 (2)												
13	1	1130	2	1380 (4)			1	1320								
14	1	1060														

[1]Smith (1995)
[2]Burns et al. (1998)
[3]Northeastern Gulf, Burns et al. (1998)
[4]Northeastern Gulf, Franks et al. (1999)

The von Bertalanffy growth equation $FL_t = L_\infty(1\text{-exp}[-K(t\text{-}t_0)])$ described the relationship between observed FL and age. Parameter estimates for this growth model are provided in Table 4. A significant difference in the overall von Bertalanffy growth models for males and females was reported by all studies and indicated that females achieved a greater theoretical asymptotic length and grew at a faster rate than males. Franks et al. (1999) reported that likelihood-ratio tests also showed that estimates of L_∞ and K were significantly different between sexes, although t_o was not significantly different.

Theoretical growth coefficients (L_∞ and t_o) reported by Thompson et al. (1992) for cobia from Louisiana were smaller than estimates reported by Franks et al. (1999) and Burns et al. (1999) for the NEGOM (Table 4). However, the estimates of K were larger in Louisiana (Thompson, 1992) than those reported by Franks et al. (1999) for both sexes and by Burns et al. (1998) for females in the NEGOM.

Asymptotic lengths for males and females taken off Virginia (Richards, 1977) were considerably larger than L_∞ values reported by Smith (1995), Thompson et al. (1995), Franks et al. (1999), and Burns et al. (1998), with the exception of male cobia from the Florida Keys and female cobia from Texas. Asymptotic length reported by Franks et al. (1999) for NEGOM males was similar to that reported for NEGOM males by Burns et al (1998), although Franks et al. (1999) reported somewhat larger lengths for females.

Overall, cobia from the Gulf appear to grow faster than those from Atlantic waters, however cobia off the Atlantic exhibit greater longevity than Gulf cobia. The differences in estimates of growth coefficients for cobia throughout their range in U.S. waters may be due to differences in geographical coverage (Franks et al. 1999) or methodological differences, e.g. sectioned otoliths verses scales. Franks et al. (1999) concluded that growth parameter estimates from their NEGOM study were appropriate for use in stock assessment studies of cobia from the NEGOM. Predicted lengths-at-age derived by the von Bertalanffy equations generally were in close agreement with observed lengths for all ages, and predicted lengths of females were greater than those of males for all ages (Thompson 1992, Smith 1995, Burns 1998, Franks 1999). All studies showed that growth in length for both sexes was relatively fast through age 2, after which growth slowed gradually.

Age Structure, Catch Curve Analysis, and Mortality

Ages 2-5 dominated the age structure of Gulf and Atlantic collections of cobia, with the exception of that of Smith (1995) who reported that 6 year-old fish also comprised a substantial portion of his sample. Franks et al. (1999) used age-length keys (male/female) to develop an estimate of the age structure of the NEGOM cobia recreational fishery (only fish greater than regulation size, ≥838 mm FL) from 1987 - 1995 and reported that ages 2 - 4 represented 85% of the catch (age 3 = 37%) and ages 5-11 represented 15%. Burns et al. (1998) found ages 3 - 5 dominated their NEGOM collections, and Thompson et al. (1992) reported that the western Louisiana sample was dominated by 2 - 4 year old cobia (75% of the sample). Thompson et al. (1992) and Franks et al. (1999) believed their sample represented the cobia recreational fishery in their respective areas at the time their studies were conducted.

Richards (1977) reported the total mortality for cobia off Virginia during the late 1960's might be excessive and suggested that a catch limit might be desirable. While there is no current estimates of fishing mortality for Virginia cobia (Mills, 2000), monitoring of the cobia fishery in Chesapeake Bay could provide data needed for effective future management of the fishery in that area.

Instantaneous total mortality estimated for NEGOM cobia using catch curve analysis of fish fully recruited into the fishery (Franks et al. 1999) showed that the age at full recruitment to the fishery was age 4. The instantaneous rate of total mortality (Z) estimated by catch curve analysis for ages 4 - 8 was 0.75 (Franks et al. 1999). Although Franks et al. (1999) believed their estimate of Z was reliable, several authors (Rounsefell and Everhart 1953, Johnson et al. 1983, Manooch et al. 1987) caution against using catch curves to predict mortality for migratory pelagic species. A fairly broad age structure and low value for Z suggest that the NEGOM population of cobia is reasonably healthy (Franks et al. 1999).

REPRODUCTIVE BIOLOGY

Sex ratio

In general, most studies found a higher percentage of females than males in their samples. The exception is Smith (1995) who found a 1:1ratio in North Carolina. Along the Gulf of Mexico, Thompson et al. (1992) reported an overall sex ratio of 1:2.1 that was skewed towards males, whereas, Franks et al. (1999) reported a predominance of females (2.7:1). Since both studies were conducted concurrently in the northern Gulf, it is difficult to explain the discrepancy, except to suggest differential segregation or a higher mortality for males east of the Mississippi River delta. Burns et al. (1998) reported an overall ratio (all areas sampled) of 2.2:1 (female:male), but noted an overwhelming number of females in the NEGOM sample (3.3:1).

Size and age at sexual maturity

Historically, few small and immature cobia of either sex have been captured due to a minimum retention size in state territorial waters and the EEZ. Thus, accurate estimates of length or age at 50% maturity cannot be made. However, reports of the smallest sexually mature male cobia observed vary from 365 mm FL and age 0 in the eastern Gulf of Mexico (Brown-Peterson et al. 2001) to 640 mm FL and age 1 in the north central Gulf of Mexico (Lotz et al. 1996). Age estimates of mature male cobia from Louisiana (Thompson et al. 1992), North Carolina (Smith 1995) and Virginia (Richards 1967) show that most males have reached sexual maturity by age 2. In contrast, females appear to reach sexual maturity at a larger size and older age. The smallest reported sexually mature female cobia range from 700 mm FL and age 1 in the eastern Gulf of Mexico (Brown-Peterson et al. 2001) to 834 mm FL and age 2 in the north central Gulf of Mexico (Lotz et al. 1996).

Table 4. Parameter estimates for the von Bertalanffy growth model for cobia Rachycentron canadum from U.S. waters. Values shown in parentheses are standard errors.

Area	Sex	n	L_∞ (mm)	K	t_0	r^2	Structure	Reference
Virginia	M	–	1,210	0.28	-0.06	–	scales	Richards (1967)[1]
	F	–	1,640	0.23	-0.08			
North Carolina	M	116	1,050	0.37	-1.08	–	otoliths	Smith (1995)[1]
			(185)	(0.04)	(0.29)			
	F	92	1,350	0.24	-1.53	–		
			(3.82)	(0.03)	(0.39)			
Carolinas	M	22	1,046	0.536	-1.085	–	"	Burns et al. (1998)[1]
	F	39	1,622	0.085	-8.596		"	"
FL Atlantic	M	24	1,138	0.195	-5.681	–		
	F	46	1,651	0.075	-7.674		"	"
FL Keys	M	17	1,170	0.230	-3.846	–		
	F	21	1,333	0.182	-4.684		"	"
FL Gulf	M	37	1,225	0.294	1.347	–		
	F	72	1,302	0.245	1.551		"	"
Northeastern Gulf	M	63	1,132	0.550	-0.759	–		
	F	194	1,302	0.461	-0.968		"	
Northeastern Gulf	M	170	1,170	0.432	-1.150	0.78		Franks et al. (1999)
			(28.08)	(0.046)	(0.173)			
	F	395	1,555	0.272	-1.254	0.87		
			(35.14)	(0.017)	(0.092)		"	
Western Louisiana	M	–	1,132	0.49	-0.49	–		Thompson et al. (1992)
	F	–	1,294	0.56	0.11		"	
Texas	M	29	929	1.43	-0.395	–		Burns et al. (1998)[1]
	F	41	1,830	0.125	-3.621			

[1] L_∞ estimates originally reported in centimeters, converted to millimeters;
- = not reported by author(s).

Female cobia appear to reach sexual maturity during their second year in Louisiana (Thompson et al. 1992) and North Carolina (Smith 1995) but not until age 3 in Virginia (Richards 1967). The differences in reported first size and age at maturity could be related to actual geographical differences or to differences in ageing techniques. Overall, it appears that males > 650 mm FL and females > 800 mm FL probably have reached sexual maturity.

Spawning Season and Gonadal Maturation

Cobia have an extended spawning season throughout their range. The spawning season has been documented using various methods, including the gonadosomatic index (GSI), observations of ovarian histology, and collection of eggs or young larvae. Table 5 summarizes the reported information on the duration of the spawning season. In general, cobia spawn during the spring and summer throughout their range. Increases in GSI values and histological observations of vitellogenic oocytes suggest that cobia are in spawning condition by April in the northern Gulf of Mexico (Thompson et al. 1992, Biesiot et al. 1994, Lotz et al. 1996, Brown-Peterson et al. 2001).

Table 5. Summary of cobia spawning seasons in United States waters.

Region	Spawning Season	Method	Reference
Virginia	June - August	GSI, histology	Joseph et al, 1964; Richards, 1967
Virginia	June - August	egg, larval collections	Joseph et al, 1964; Mills, 2000
North Carolina	May - July	GSI	Smith, 1995
North Carolina	May - August	egg, larval collections	Hassler and Rainville, 1975; Smith, 1995
South Carolina	May - August	egg, larval collections	Shaffer and Nakamura, 1989
North central Gulf of Mexico	April - September	GSI, histology	Biesiot et al., 1994; Lotz et al., 1996; Brown-Peterson et al., 2001
North central Gulf of Mexico	May - September	egg, larval collections	Ditty and Shaw, 1971
Louisiana	April - August	GSI, histology	Thompson et al., 1992
Texas	May - September	egg, larval collections	Baughman, 1950; Finucane et al. 1978

The peak spawning time was variously reported as April (Biesiot et al. 1994), May (Lotz, et al. 1996), June (Thompson et al. 1992) and May through July (Brown-Peterson et al. 2001). While the spawning season appears to extend for six months in the northern Gulf of Mexico, the percentage of females in reproductive condition by September is greatly reduced (Brown-Peterson et al. 2001). However, collection of cobia eggs and young larvae from May through September throughout the northern Gulf of Mexico (Ditty and Shaw 1971, Finucane et al. 1978) confirm the six month spawning season in the region.

Cobia along the Atlantic coast of the southeastern United States have a shortened reproductive season relative to Gulf of Mexico fish (Table 5). Smith (1995) reported a May through July spawning season in North Carolina, with a peak in June, based on GSI values. Egg and larval collections from North and South Carolina (Hassler and Rainville 1975, Smith 1995, Shaffer and Nakamura 1989) confirm a four month, May through August, spawning season. However, Brown-Peterson et al. (2001) reported that cobia from Morehead City, North Carolina to Cape Canaveral, Florida were in reproductive condition by April based on histological observations. Cobia in the Chesapeake Bay, Virginia region appear to have a June through August reproductive season, based on GSI values (Joseph et al. 1964), ovarian observations (Richards, 1967) and collections of eggs and larvae (Joseph et al. 1964, Mills, 2000).

Some female cobia in the northern Gulf of Mexico do not appear capable of spawning during the entire six month reproductive season. Female cobia with ovaries in the spent and regressed classes were observed in July and August during the course of several studies (Thompson et al. 1992, Biesiot et al. 1994, Lotz et al. 1996, Brown-Peterson et al. 2001). Similarly, some cobia were not in spawning condition until May or June (Brown-Peterson et al. 2001). This phenomena has not been reported along the Atlantic coast of the southeastern United States, which may be a result of the shorter reproductive season in that area.

Histological observations of male cobia suggest that spermatogonial proliferation and spermatogenesis is a year-round process (Brown-Peterson et al. in review). Spermatogonial proliferation takes place from the end of the reproductive season in September until the beginning of the next season in April while spermatogenesis occurs from February through August. Although male cobia always contained sperm in the testis (Brown-Peterson et al. 2001; in review), and may be capable of year-round spawning, females were only found in the late developing ovarian class from April through September.

Cobia are capable of spawning several times during the reproductive season. While multiple spawning was first proposed by Richards (1967), Brown-Peterson et al. (2001) were the first to provide definitive evidence of multiple spawning in the form of post ovulatory follicles (POF) in the ovaries of fish with fully mature, vitellogenic oocytes. Additional evidence of multiple spawning is ovaries containing oocytes undergoing final oocyte maturation (FOM) concurrent with fully mature, vitellogenic oocytes (Lotz et al. 1996, Brown-Peterson et al. 2001).

Spawning Location

Definitive information on the location of cobia spawning is lacking. In the northern Gulf of Mexico, no cobia with hydrated oocytes have been captured (Thompson et al. 1992, Lotz et al. 1996, Brown-Peterson et al. 2001), suggesting that sampling does not occur around spawning locations. Several cobia with hydrated oocytes have been captured from the Chesapeake Bay, Virginia area (J. Olney, VIMS, pers. comm.). The location of these captures corresponds with collections of eggs and larvae, suggesting that cobia in Chesapeake Bay spawn at the mouth of the Bay and immediately offshore of the Virginia Capes (Joseph et al. 1964, Mills, 2000). Egg and larval collections from North Carolina suggests spawning near inlets (Smith 1995) as well as 25 to 50 km offshore (Hassler and Rainville 1975). Offshore spawning was also indicated in South Carolina (Shaffer and Nakamura 1989) as well as throughout the northern Gulf of Mexico (Baughman 1950, Dawson 1971, Finucane et al. 1978, Ditty and Shaw 1982). However, collections of newly spawned eggs and recently hatched larvae in Crystal Bay, Florida (Ditty and Shaw 1982) suggest cobia may also spawn inshore in 6 m of water in the northern Gulf of Mexico. Overall, few eggs or larvae have been obtained in any collections, leading to further confusion regarding the exact location of cobia spawning.

Batch Fecundity and Spawning Frequency

Early reports of cobia fecundity were inaccurate, as they attempted to estimate the fecundity of a multiple spawning fish by counting all vitellogenic oocytes rather than just hydrated oocytes (Richards 1967, Lotz et al., 1996). The lack of cobia containing hydrated oocytes resulted in Brown-Peterson et al. (2001) using cobia with oocytes undergoing FOM for estimates of batch fecundity. Fecundity was determined by counting all oocytes > 700 μm using the volumetric method and by counting the number of oocytes undergoing FOM in histological sections. Batch fecundity was significantly, positively related to both fork length and ovary-free body weight (OFBW). Mean batch fecundity estimates were not significantly different among methods and varied from 377,000 ± 64,500 to 1,980,500 ± 1,598,500 eggs (Brown-Peterson et al. 2001). Relative batch fecundity was not significantly different among months during the spawning season and averaged 29.1 ± 4.8 eggs/g OFBW for the histological method and 53.1 ± 9.4 eggs/g OFBW for the volumetric method (Brown-Peterson et al. 2001). These relative batch fecundity values compare favorably with those of other pelagic species such as wahoo (*Acanthocybium solandri*, Brown-Peterson et al. 2000), tripletail (*Lobotes surinamensis*, Brown-Peterson and Franks, in press), southern bluefin tuna (*Thunnus maccoyii*, Farley and Davis 1998) and yellowfin tuna (*T. albacares*, Schaefer 1996).

While the multiple spawning nature of cobia has been acknowledged for many years, actual estimates of the spawning frequency of cobia have only recently been reported. Brown-Peterson et al. (2001) examined the percentage of cobia with fully mature ovaries containing either POF or FOM and determined that cobia from the north-central Gulf of Mexico and from the Atlantic Coast of the southeastern United

States spawn once every five days. Cobia from Texas were estimated to spawn once every 9 to 12 days, although this spawning frequency was not significantly different from other areas within the Gulf of Mexico (Brown-Peterson et al. 2001). However, these estimates suggest that cobia spawn less frequently than other pelagic species such as southern bluefin tuna (Farley and Davis 1998), yellowfin tuna (Schaefer 1996), wahoo (Brown-Peterson et al. 2000) and narrow barred Spanish mackerel (*Scomberomorus commerson*, McPherson 1993).

Potential annual fecundity of cobia can be estimated by combining the batch fecundity and spawning frequency estimates. Thus, a 20 kg cobia from the north-central Gulf of Mexico may potentially spawn 20,952,000 to 38,232,000 eggs between April and September. The shorter reproductive season along the southeastern United States would result in a potential annual fecundity for the same size female of 14,200,800 to 25,912,800 eggs from mid-April through mid-August. Finally, the lower spawning frequency of cobia in Texas would result in a potential annual fecundity of the same 20 kg female of 8,730,000 to 21,240,000 eggs from April through September.

Areas of Future Research

While much has been learned about the biology of cobia during the past 20 years, there is a lack of information in several critical areas. The population age structure, growth parameters, and harvest levels of cobia warrant continued monitoring and assessment throughout its U.S. range. Accurate estimates of the size and age of sexual maturity for both male and female cobia are necessary, particularly with the increase in recreational exploitation of cobia and the development of region-wide fishery management plans. While the knowledge of spawning seasonality and gonadal maturation of cobia appears adequate, the lack of accurate information on spawning locations needs to be addressed. Additional information on batch fecundity, particularly by region, will give a better understanding of spawning stock dynamics of cobia. The fecundity values provided by Brown-Peterson et al. (2001) are a good first approximation, but are based on a relatively small sample size (N = 39) of combined samples from the Atlantic Coast of the southeastern United States (North Carolina to Florida) and the northern Gulf of Mexico (Florida to Louisiana). The striking differences in spawning frequency within the Gulf of Mexico needs to be researched further, with additional samples from all areas of the Gulf. Future biological studies of cobia in U.S. waters also should include a genetic assessment of the cobia population(s) in Gulf and U.S. Atlantic waters.

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