

ASPECTS OF THE REPRODUCTIVE BIOLOGY OF THE WEAKFISH, *CYNOSCION REGALIS* (SCIAENIDAE), IN NORTH CAROLINA^{1,2}

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ABSTRACT

The weakfish, *Cynoscion regalis*, has an extended spawning season in North Carolina's inshore waters (males are ripe March to August, and females are ripe April to August). Peak spawning activity occurs from late April through June. The extended spawning season throughout the range is a major factor in variability of size within a year class.

Published accounts cite attainment of sexual maturity at age II for males and age III for females. I conclude that weakfish of both sexes reach sexual maturity as yearling fish, although some smaller members of a year class do not mature until their second year.

Weight and length of weakfish are better indicators of fecundity than is age (higher correlation coefficients). A female weakfish of 500 mm standard length produces slightly over two million eggs.

The weakfish, *Cynoscion regalis*, is a littoral species of commercial and sport importance in the middle Atlantic states from North Carolina to New York (Bigelow and Schroeder 1953). Welsh and Breder (1923), Higgins and Pearson (1928), Hildebrand and Schroeder (1927), Hildebrand and Cable (1934), Pearson (1941), Roelofs (1951), and Harmic (1958) described portions of the reproductive biology of weakfish. The most recent data concerning reproductive biology of this species in North Carolina were in Hildebrand and Cable (1934).

The decline in commercial catch of weakfish between 1945 and the mid-1960's and speculation as to its cause(s) (Roelofs 1951; Perlmutter 1959; Fahy 1965a, b; Brown and McCoy 1969; Joseph 1972) indicated the need for a biological study of the weakfish along the Atlantic coast (Nesbit 1954; Perlmutter et al. 1956; Massmann et al. 1958). I undertook a study of the weakfish in North Carolina (1967-70) to provide biological data from which recommendations for management could be formulated. This paper presents data on reproduction of weakfish pertaining to: 1) spawning season, 2) age and size at which sexual maturity is attained, 3) fecundity relationships, and 4) possible role of reproductive biology in the observed population decline along the eastern seaboard.

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MATERIALS AND METHODS

A total of 3,635 weakfish were obtained for biological examination from the area bounded by Cape Hatteras and Cape Fear, N.C. Landings of pound nets, haul seines, gill nets, and shrimp trawls in the vicinity of Cape Hatteras, between June 1967 and November 1969, contributed 1,606 specimens (Figure 1). An additional 2,029 weakfish were obtained between June 1967 and January 1970 from trawler landings in Morehead City and Beaufort, and from haul seines landing in Atlantic and Sea Level (Figure 1).

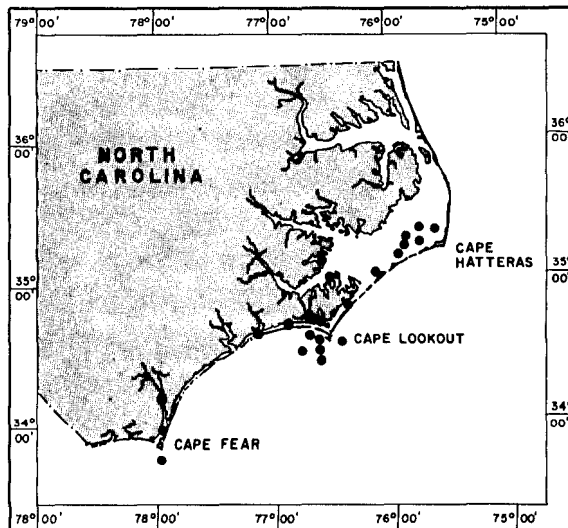


FIGURE 1.—Location of sampling sites included in 1967 to 1970 collections of weakfish from North Carolina waters.

Scale samples were taken from under the tip of the pectoral fin below the lateral line of 2,159 weakfish for age determination. Age-group or age-class cited herein refers to the number of annuli on scales. Weight in grams and length (total, fork, and standard) in millimeters were recorded from all specimens.

Sex and maturation stage of gonads were assigned after macroscopic examination of the gonads using a modification of the classification of Kesteven (1960). Histological sections of representative gonads in each stage provided verification of maturation class assignment (Table 1).

Gonad index indicated duration and peak of spawning season as well as the age and size at which weakfish attain sexual maturity. Gonads from 571 females and 117 males from the Hatteras and Morehead City areas were preserved in 10% Formalin⁴ and used for analysis of gonad condition. The index value equals the weight of the preserved gonad, to the nearest 0.01 g, divided by the body weight of the fish, to the nearest 1.0 g, times 100. It represents the percent contribution of gonads to total fish weight.

Twenty-two female weakfish with well-developed oocytes (mature ovaries) provided the basis for fecundity relationships. Age-groups I through IV are represented by 20 fish collected between 25 May and 13 June 1969, from Pamlico Sound. Age-group 0 is represented by two females collected near Morehead City on 4 June 1968. The preserved ovaries were blotted dry and weighed to the nearest 0.01 g. One ovary from each pair was randomly selected for sampling. A thin slice (1-2 mm) was cut from the anterior, middle, and posterior regions of the ovary. These slices were weighed to the nearest 0.0001 g and placed in Gilson's solution for 8 to 12 h to facilitate egg separation from connective tissue (Bagenal 1967). Then the sections were rinsed with tap

⁴Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

water and teased apart with dissecting needles. The separated egg samples were placed in a petri dish which was areally divided as a 6 × 6 grid and stirred until equally distributed within the dish before counting. Specific grid sectors were randomly selected. The portion of the sample counted ranged from one-ninth in larger ovaries to a total count in small ovaries. Counts were made using a dissecting microscope and included all eggs having yolk deposition equal to or greater than the diameter of the oil globule.

Treatment of fecundity data included analysis of variance for age-groups 0 through IV (Steel and Torrie 1960) and linear regression. Fecundity was related to total length (TL) and standard length (SL) of the fish in millimeters using the equation,

$$F = aL^b$$

where F = fecundity,

L = total or standard length of the fish,

a, b = constants for the equation.

Fecundity was related to fish weight in grams using the equation,

$$F = a + bW$$

where F = fecundity,

W = fish weight,

a, b = constants for the equation.

RESULTS

Monthly summaries of testes maturation classes revealed an extended spawning season and an early summer peak in spawning for male weakfish. Over one-fourth of the males sampled from March through August were ripe running (Table 2) and over one-half were ripe running from April through July. During September and October,

TABLE 1.—Gonad stage designations and macroscopic condition of the male drumming muscle used in describing weakfish maturity.

Female		Male		
Gonad stage ¹		Gonad stage ¹		Condition of drumming muscle
Immature	(I)	Immature	(I)	White, undeveloped
Mature	(II, III, and IV)	Mature	(II and III)	Pink, beginning to thicken
Ripe	(V)	Ripe	(IV)	Red, thickened
Ripe running	(VI)	Ripe running	(V and VI)	Deep red, very thick
Ripe spent	(VII)	Ripe spent	(VII)	Red to deep red, thinner
Spent	(VIII)	Spent	(VIII)	Mottled red to pale red, thinner
Spent resorbing	(VIII and II)	Spent resorbing	(VIII and II)	Pink, thin
Resorbing	(I for larger fish)	Resorbing	(I for larger fish)	Pink to white, thin

¹Roman numerals indicate the corresponding stage for the Kesteven scheme (1960).

TABLE 2.—Gonad condition for male weakfish from North Carolina as a percent of the monthly sample.

Month	Number	Immature	Mature	Ripe	Ripe running	Spent	Ripe spent	Spent resorbing	Resorbing
January	13	30.8	38.4	23.1	7.7				
March	201	3.5	30.3	39.8	26.4				
April	4				100.0				
May	32				100.0				
June	121	6.6		3.3	90.1				
July	137	13.1		3.7	80.3	2.9			
August	173	34.7	1.2	5.3	46.8	12.1			
September	189	20.1	0.5		4.2	47.6	13.8	13.8	
October	76	26.3			2.6	46.1	7.9	14.5	2.6
November	11	27.3						72.7	
December	11		27.3	72.7					
Total	968								

45% of the males were in the spent condition while only 4.2% and 2.6% respectively were ripe running. Male weakfish examined during November and December were not in the ripe running stage. Testes of fish collected in December were developing, and the drumming muscle was enlarging for the next spawning season (Table 1).

The gradual progression of ovarian maturation state from mature (dominant in March) to resorbing (dominant in December) suggests an extended spawning season for female weakfish. Females were in the ripe or ripe running stage from March through September (Table 3). From April through July, over one-fourth of the females were in the ripe category. Female weakfish completed spawning by October. Over 30% of the ovaries were in the spent resorbing condition during September and October.

Evidence of multiple spawning during a given season by individual fish in age-groups I and older was found during analysis of ovarian condition. Ovaries contained mature follicles during April and May with clusters of immature follicles interspersed among translucent oocytes. These ovaries were staged as ripe or ripe running depending upon the extrusibility of oocytes. During June, 26.6% of the ovaries were classified as ripe

spent (Table 3). These ovaries still possessed mature follicles, but were flaccid relative to those of April and May, showed hemorrhage, and the clusters of immature follicles were maturing (enlarging). Ovaries staged as ripe or ripe running in July and August were rather flaccid relative to ovaries collected in the spring and did not have a hemorrhagic appearance. In late August and September, the ovaries possessed spent characteristics including atresia of remaining follicles. In the fall, ovaries exhibited further resorption of follicles and flaccid condition. The ovaries gradually resumed firmness after resorption.

The distribution of gonad index for male and female weakfish of all age-classes was unimodal with the greatest contribution of gonad to total body weight occurring in the early summer. Testicular indices peaked in May at 2.6% and declined to 0.5% in July (Figure 2). After July no change in gonad index occurred until the next spawning season. Ovarian indices reached maximum values in May (8.3%) and declined to an autumn low of less than 0.1% in September (Figure 2). Both male and female indices from April through June were considerably greater than those of either March or July. Mean monthly gonad indices reveal the major spawning period to be April through June. However, some males

TABLE 3.—Gonad condition of female weakfish from North Carolina as a percent of the monthly sample.

Month	Number	Immature	Mature	Ripe	Ripe running	Spent	Ripe spent	Spent resorbing	Resorbing
January	7	57.1	42.9						
March	148	13.5	79.7	6.8					
April	9		33.3	66.7					
May	57	1.8	38.6	56.1	3.5				
June	173	26.6	4.6	31.8	4.0	5.8	26.6	0.6	
July	186	24.2	9.1	27.4	5.9	13.4	17.2	2.2	0.5
August	221	35.7	1.4	15.4	0.9	31.7	11.7	3.2	
September	128	14.0		0.8	1.6	40.6		41.4	1.6
October	62	33.9				12.9		32.2	21.0
December	9		22.2						77.8
Total	1,000								

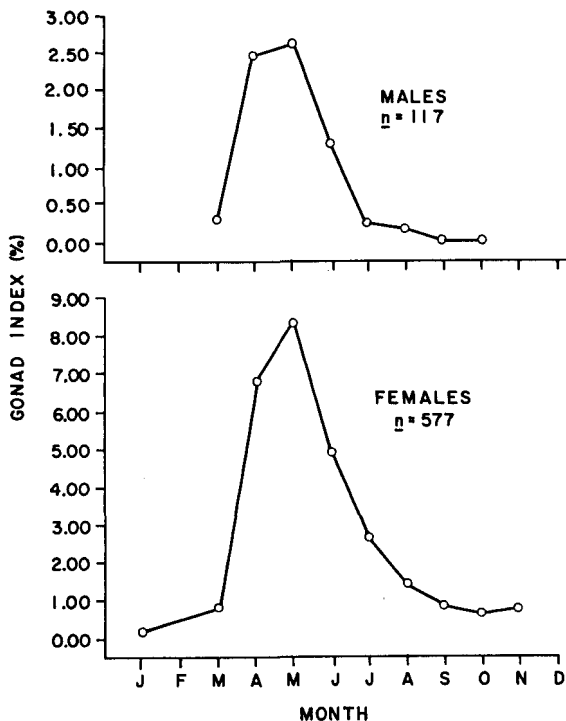


FIGURE 2.—Mean monthly gonad index for male and female weakfish of all age-classes expressed as percent body weight.

and females were in spawning condition from March through September.

Age 0 weakfish (no scale annulus) exhibited a seasonal gonad index pattern similar to that of older fish. The peak index values for age 0 females occurred in June, a month later than age I females (Figure 3). Gonads of age 0 females accounted for only 4% of the total body weight whereas they represented over 8% of body weight in age I females.

Over one-half of the age 0 weakfish collected were classified as mature (Table 4). Of the 201 age 0 females, 105 or 52% were mature. Of the

TABLE 4.—Number of immature and mature age-group 0 weakfish from North Carolina by month.

Month	Female		Male	
	Immature	Mature	Immature	Mature
January	4	2	4	3
March	30	68	8	115
May	1	0	0	4
June	14	9	1	17
July	1	0	3	0
August	6	0	24	5
September	18	4	38	6
October	20	13	19	11
November	2	8	3	2
December	0	1	—	—
Total	96	105	100	163

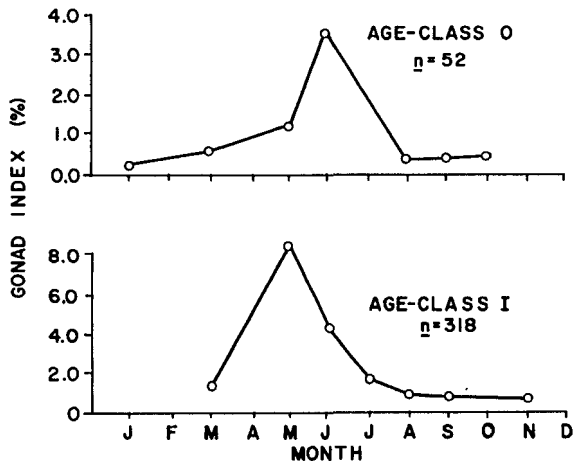


FIGURE 3.—Mean monthly gonad index for female weakfish of age-class 0 and I expressed as percent body weight.

263 age 0 males, 163 or 62% were mature. Deletion of obvious young of the year fish collected after 3 to 4 mo growth elevated the percent mature to 91 for males and 68 for females in age-group 0.

Male weakfish attain sexual maturity at a smaller size than do female weakfish and both sexes attain sexual maturity at smaller size in the vicinity of Morehead City than in Pamlico Sound (Table 5). The standard length range in which 50% of the weakfish were classified as mature, ripe, or ripe running was considered the size at which sexual maturity is attained. Weakfish less than 100 mm SL were not sexually mature in either area. Males from the Morehead City area reached the 50% criterion at about 130 mm SL ($n = 1$). Male weakfish from Pamlico Sound fulfill the criterion for population maturity at about 150 mm SL ($n = 13$, 61% mature). Female weakfish from the Morehead City area attain maturity at about 145 mm SL ($n = 11$, 54% mature), while female weakfish from the Pamlico Sound area attain sexual maturity at about 190 mm SL ($n = 28$, 57% mature).

Size of the individual fish rather than age is the dominant factor affecting the attainment of sexual maturity by weakfish. In the vicinity of Morehead City, male weakfish of age-group I but less than 170 mm SL were mature ($n = 12$, 1 immature) (Table 6). All age II male weakfish examined from that area were mature ($n = 26$). Females of 175 mm SL or larger from the same area with no annulus on their scales were mature. There was only one immature fish among

TABLE 5.—Relationship of standard length and percent mature for weakfish from North Carolina by sex and area (1967-69).

Standard length ¹ (mm)	Female				Male			
	Pamlico Sound		Morehead City		Pamlico Sound		Morehead City	
	Number	% mature	Number	% mature	Number	% mature	Number	% mature
≤100			1	0			42	0
105					1	100		
110							2	0
115							7	14
120							2	0
125	4	0	1	0	5	20	2	0
130	4	0			4	0	1	100
135	3	0			9	33	5	60
140	5	20	4	25	12	33	3	67
145	15	7	11	24	9	11	9	56
150	18	22	6	33	13	61	9	67
155	15	7	21	67	15	47	15	80
160	12	42	29	76	18	56	25	96
165	20	15	31	87	24	83	32	100
170	26	23	20	90	19	58	40	95
175	24	21	23	100	15	87	33	97
180	19	26	26	85	31	77	24	100
185	27	48	24	100	20	85	28	100
190	28	57	24	96	34	77	22	100
195	45	69	29	90	36	94	40	100
200	16	81	23	96	25	100	28	100
205	27	93	27	96	32	97	35	100
210	18	78	16	100	14	100	19	100
215	20	85	17	100	13	100	21	100
220	10	80	11	100	15	100	10	100
225	10	100	12	100	7	100	4	100
230	6	100	8	100	6	100	7	100
235	9	100	3	100	4	100	4	100
240	5	100			5	100	3	100
>240	83	99	16	100	25	100	1	100
Total	469		383		411		473	

¹Midpoint of length interval (102.6 to 107.5 = 105, etc.).

TABLE 6.—Relationship of age-group and standard length to percent sexually mature by sex for weakfish from the vicinity of Morehead City, N.C. (1968-69).

Standard length ¹ (mm)	Age-group 0				Age-group I				Age-group II			
	Male		Female		Male		Female		Male		Female	
	Number	% mature	Number	% mature	Number	% mature	Number	% mature	Number	% mature	Number	% mature
≤100	42	0	1	0								
110	2	0										
115	7	14										
120	2	0										
125	2	0	1	0								
130	1	100										
135	4	50			1	100						
140	2	50	4	25	1	100						
145	7	43	9	44	2	100	2	100				
150	7	71	5	40	2	50	1	0				
155	13	77	19	63	2	100	2	100				
160	22	96	29	76	3	100						
165	31	100	26	85	1	100	5	100				
170	35	97	9	78	5	80	11	100				
175	14	100	13	100	19	98	10	100				
180	7	100	5	100	16	100	21	81	1	100		
185	4	100	1	100	24	100	22	100			1	100
190					22	100	23	96			1	100
195	1	100			38	100	29	90	1	100		
200					26	100	22	96	2	100	1	100
>200					82	100	81	99	22	100	29	100
Total	203		122		244		229		26		32	
Mean		67		73		99		95		100		100

¹Midpoint of length interval.

the female weakfish of age-group I less than 175 mm SL ($n = 21$). All females in age-group II were mature ($n = 32$). Males of age-group 0 from Pamlico Sound were sexually mature at 150 mm SL while males in age-group I reached maturity at

135 mm SL (Table 7). All age-group II males examined from this area were sexually mature ($n = 89$). Females of age-group 0 in the Pamlico Sound area reached sexual maturity at 175 mm SL ($n = 3$, 1 immature) while age-group I females

TABLE 7.—Relationship of age-group and standard length to percent sexually mature by sex for weakfish from Pamlico Sound, N.C. (1967-69).

Standard length ¹ (mm)	Age-group 0				Age-group I				Age-group II			
	Male		Female		Male		Female		Male		Female	
	Number	% mature	Number	% mature	Number	% mature	Number	% mature	Number	% mature	Number	% mature
105	1	100										
125	4	25	3	0	1	0	1	0				
130	2	0	3	0	2	0	1	0				
135	6	17	3	0	3	67						
140	9	22	3	0	3	67	2	50				
145	5	0	12	0	4	25	3	33				
150	12	58	10	10	1	100	8	38				
155	7	43	9	11	8	50	6	0				
160	4	50	5	40	14	57	7	43				
165	4	100	5	20	20	80	14	7			1	100
170	1	100	6	17	18	55	20	25				
175	2	100	3	67	13	85	21	14				
180			3	100	31	77	16	12				
185					19	84	27	48	1	100		
190			1	0	33	76	25	52	1	100		
195	1	100	1	100	31	94	44	68	4	100		
200	1	100			17	100	13	85	7	100		67
205					19	95	25	92	12	100	2	100
210					7	100	15	73	7	* 100	3	100
215					4	100	14	93	9	100	6	67
220					5	100	5	60	10	100	5	100
>220					9	100	33	100	38	100	80	99
Total	59		67		262		300		89		100	
Mean		44		18		80		56		100		96

¹Midpoint of length interval.

were mature at a length of 190 mm ($n = 25$, 52% mature) (Table 7).

Average estimated fecundity increased with age from 45,000 eggs for age 0 females to 1,726,000 eggs for age IV females. The increases in fecundity with age were significant ($F = 15.64$, $df = 17.4$; $P < 0.01$; Table 8). Variation within individual age groups was great with the standard deviation approaching one-third of the mean estimated fecundity. Relative fecundity, the number of eggs per gram of ovary, decreased from 37,650 at age 0 to 14,867 at age IV.

Regression analysis indicated significant relationships between fecundity and fish length and weight. The equations describing the relationships and coefficients of determination are:

$$F = 0.116 SL^{2.7755}, r^2 = 0.85;$$

$$F = 0.152 TL^{2.6418}, r^2 = 0.86 \text{ (Figure 4);}$$

$$F = 21,198 + 1,279 W, r^2 = 0.88.$$

TABLE 8.—Fecundity estimates and relative fecundity for 22 weakfish from North Carolina and analysis of variance results for age versus fecundity.

Age-group	Number examined	Mean fecundity estimates	Standard deviation	Mean no. of eggs per gram of ovary	Standard length range (mm)	Anova				
						Source	df	Sum of squares	Mean square	F
0	2	44,880	10,693	37,650	145-160	Age	4	5.219×10^{12}	1.305×10^{12}	15.64**
I	8	285,740	105,600	21,225	190-268	Error	17	1.418×10^{12}	8.341×10^{10}	
II	7	579,660	302,700	19,400	245-308	Total	21	6.637×10^{12}		
III	2	491,700	186,900	15,150	292-335					
IV	3	1,725,920	614,300	14,867	395-480					
Total	22									

**Probability less than 0.01.

DISCUSSION

Weakfish spawn in or near the various inlets along the coast of North Carolina (Welsh and Breder 1923; Higgins and Pearson 1928; Hildebrand and Cable 1934) and also in Pamlico Sound. Earlier authors did not include sounds and bays as probable spawning sites since no female weakfish in spawning condition had been taken from inshore waters of North Carolina (Roelofs 1951). Higgins and Pearson (1928) reported a few weakfish with "free running ripe eggs" in Pamlico Sound. Twenty-four female weakfish in the ripe running condition were obtained from Pamlico Sound, and this indicates weakfish may also spawn in sounds and bays. These areas may be at the edge of the spawning zone, however.

Spawning activity in coastal waters north of North Carolina is cited by Hildebrand and

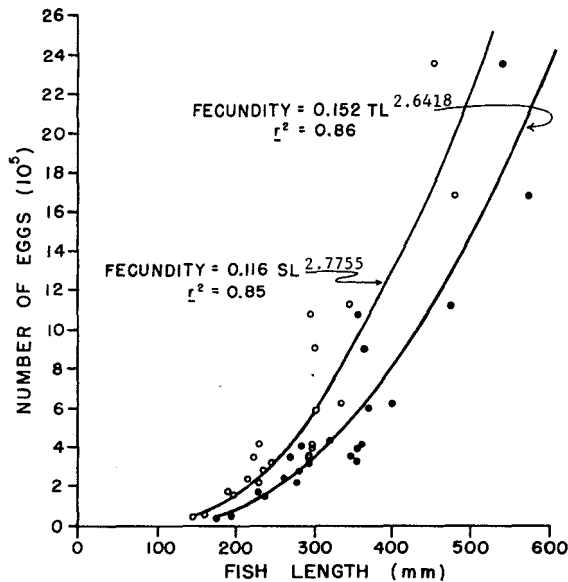


FIGURE 4.—Relationship of weakfish fecundity to fish length based upon data from 22 females.

Schroeder (1927), Pearson (1941), and Massman (1963) for Chesapeake Bay; by Parr (1933), Daiber (1954), Harmic (1958), and Thomas (1971) for Delaware Bay; by Nesbit (1954) and Perlmutter et al. (1956) for New York and New Jersey waters; and by Bigelow and Schroeder (1953) for the Gulf of Maine. However, the magnitude of spawning in northern areas is unknown. Progeny from spawning activity north of Chesapeake Bay are considered insufficient to maintain the northern stock (Harmic 1958), and young from the Carolinas and Chesapeake Bay are thought to be recruited to the northern population as age III or older fish (Pearson 1941; Nesbit 1954; Perlmutter et al. 1956; Harmic 1958). The validity of this supposition remains to be documented.

Mature weakfish enter the inshore waters, sounds, and bays of North Carolina in early spring (Hildebrand and Schroeder 1927; Hildebrand and Cable 1934; Roelofs 1951). Fertilized eggs have been taken in Delaware Bay when water temperatures ranged from 17° to 26.5°C and at salinities from 12.1 to 31.3‰ (Harmic 1958).

Weakfish apparently have an extended spawning season in North Carolina waters as reported by Welsh and Breder (1923), Higgins and Pearson (1928), Hildebrand and Cable (1934), and Pearson (1941). Distributional data for weakfish eggs and larvae are lacking in North Carolina waters. Peak spawning activity occurs from late April

through June as indicated by gonad condition and gonadal index. Females appear to spawn the major portion of their eggs in May or June with a second spawn of smaller magnitude possibly occurring in late July or August. Thus, weakfish of a given year class may vary considerably in size due to their extended spawning season and multiple spawning by females.

Weakfish males and females probably attain sexual maturity as 1-yr-old fish throughout their geographic range, though some of the smaller members of a year class may not mature until their second year of life. Weakfish in North Carolina waters were previously reported to reach sexual maturity at age II for males and age III for females (Taylor 1916; Welsh and Breder 1923; Higgins and Pearson 1928), and subsequent papers have reiterated these ages without verification. Higgins and Pearson (1928) reported no mature females less than 200 mm fork length (approximately 170 mm SL) and that a fork length of 230 mm was attained before 50% of the female weakfish mature in Pamlico Sound. This size group was allocated to age-group III without examining scales for annuli. I consider their allocation of age-classes to be in error on the basis of data presented here and in Merriner (1973). I found 21 mature female weakfish 170 mm SL in samples from Pamlico Sound and 90 mature female weakfish of the same size from the vicinity of Morehead City. Over one-half of the female weakfish were mature at 190 mm SL in samples from Pamlico Sound, and male weakfish become sexually mature at a smaller size than females. Weakfish spawned in May or June would be mature the following May or June. Those fish spawned in late July or August probably would not be sexually mature until late summer of the year following their hatch or the following spring. Scrap samples from pound nets in Chesapeake Bay contained mature female weakfish measuring 170 to 250 mm TL during late spring and summer months (McHugh 1960). Maturation at a small size is also likely for fish from more northerly areas (Daiber 1954; Thomas 1971).

No evidence of alternate year spawning was found even in the oldest specimens examined. All of the females of age III or older were either in spawning condition or mature during early summer. However, some of the older weakfish in the population may not migrate inshore during spring and summer.

Weakfish are characterized by high fecundity.

In Delaware Bay a female weakfish, 190 mm SL, contained a total of 267,500 eggs and would release approximately 52,000 eggs at one spawning (Daiber 1954). My estimates of fecundity for females of a similar size are equivalent to the total egg production figure for Delaware Bay. Fecundity increases by approximately 106,000 eggs for each 100 g of body weight for weakfish in Delaware Bay, while my data indicate an increase of 127,900 eggs per 100 g of body weight.

The variation in fecundity per age-group is best explained by the size range present in the samples of each age-group. Regression analysis showed a significant relationship between fecundity and fish length (coefficient of determination = $r^2 = 0.85$) and between fecundity and fish weight ($r^2 = 0.88$). The average range of standard length for all females in age-groups 0 to IV was 57 mm. High variability in fecundity estimates for age-groups is expected due to the range in fish size and variation in gonad size among fish of the same size (Bagenal 1967).

It is highly unlikely that weakfish experienced a synchronous failure or severe depression of embryonic or larval survival in all spawning areas. Harmic (1958) analyzed the early life history of weakfish in Delaware Bay. Fertilized eggs are pelagic and measure from 0.87 to 0.99 mm in diameter. Weakfish larvae emerge after about 40 h at water temperatures of 68° to 70°F and average 1.8 mm SL. Soon after hatching, the demersal larvae disperse into the nursery areas. Throughout the coastal waters from North Carolina to at least New York, anomalous water conditions (such as rapid changes in salinity, temperature, or dissolved oxygen) may occur in small areas due to local weather phenomena or industrial-domestic development. Hurricanes, however, may affect the entire eastern seaboard (tropical storm Agnes—1972) or portions of it (Hurricane Camille—1969) with the greatest impact occurring in the estuarine areas (i.e., weakfish nursery). The extended spawning season of weakfish would tend to minimize any effect of a short-term calamity upon a local population.

Tolerance of weakfish eggs and larvae to temperature, salinity, dissolved oxygen, etc., remains poorly known. According to data compiled by Harmic (1958), natural fluctuations in the estuary approach the ranges that are detrimental to weakfish survival. For Delaware Bay and presumably throughout its range, the variation in water parameters due to natural phenomena

alone may largely explain fluctuations in the weakfish population abundance and year class strength.

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