Erik J. Olsen. **MATURATION AND FECUNDITY OF ROANOKE/ALBEMARLE STRIPED BASS (*Morone saxatilis*)** (Under the direction of Roger A. Rulifson). Department of Biology, October 1991.

Since the early 1940s, several investigators have determined age to maturity schedules for female striped bass (*Morone saxatilis*) at various locations along the eastern seaboard. Techniques utilized by Specker and colleagues at the University of Rhode Island suggest that methods used by Merriman (1941) and Lewis (1962) may underestimate the number of females entering the spawning population at an early age (e.g., ages 3 and 4). Such information is important for developing management plans involving harvest quotas and size limits to allow females to reach spawning age before harvest. At the present time, managing the harvest of striped bass within the Roanoke River and Albemarle Sound, North Carolina, is controversial; harvest quotas and size limits based on Chesapeake Bay maturation schedules might be implemented if information on the present age to maturity rate of Roanoke fish is not determined. The objective of my study was to establish a maturity schedule for Roanoke female striped bass participating in the 1989 and 1990 spawning seasons, and estimate the potential fecundity of the fish as a function of size and age.

A total of 265 female striped bass was collected from the Roanoke/Albemarle system during the pre-spawning and spawning seasons (March through May) of 1989 and 1990. Length, total weight, and gonadal weight were recorded for each fish. A portion of each ovary was removed and histologically prepared for oocyte measurement. Potential fecundity was determined gravimetrically. Ages were determined using scales. Females ranged in size from 344 to 1172 mm FL and 2 to 16 years of age. Maturity estimates using the methods of Merriman (1941), Lewis (1962), and Specker et al. (1987)

were very similar and not significantly different, indicating that about 44% of age 3 females were sexually mature, and all females examined were mature by age 6. Regression analysis indicated that age 3 females produce approximately 200,000 eggs. A curvilinear relationship exists between fish age and the number of eggs produced, with greatest increase between age 6 and age 10. These data suggest that Roanoke female striped bass may mature at an earlier age than those from other systems. The rate of maturity by age compared to previous Roanoke/Albemarle studies appears to be increasing. During the 1950s, only 4% of age 3 females were mature; while in the early 1980s, approximately 18% of age 3 females were mature. This trend may be due to slight differences in the earlier studies, or to unknown factors perhaps related to environmental stress, fishing pressure, and/or genetic differences.

MATURATION AND FECUNDITY OF ROANOKE RIVER/ALBEMARLE SOUND STRIPED BASS (*Morone saxatilis*)

A Thesis

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by

Erik J. Olsen

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by

Erik J. Olsen

APPROVED BY:

DIRECTOR OF THESIS

Roger A. Rulifson, Ph.D.

THESIS COMMITTEE

Gerhard W. Kalmus, Ph.D.

Charles W. O'Rear, Ph.D.

Jennifer L. Specker, Ph.D.

CHAIRMAN OF THE DEPARTMENT OF BIOLOGY

Charles E. Bland, Ph.D.

DEAN OF THE GRADUATE SCHOOL

Diane M. Jacobs, Ph.D.

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To my loving wife Jody, for her sense of humor when I came home smelling like fish, for her undying love, patience, and understanding during all those days/evenings/ nights that I was away working on this project, THANK YOU!

(P.S. Zachary, Daddy says Hi!)

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

Historically, the striped bass (*Morone saxatilis*) has sustained economically important recreational and commercial fisheries along the Atlantic coast. The species ranges from the St. Lawrence River in Canada (Magnin and Beaulieu 1967) to the St. Johns River in northern Florida (Raney 1952) and in tributaries along the Gulf of Mexico from Florida to Louisiana. It is most abundant from Massachusetts to North Carolina (Merriman 1941). In 1879, the striped bass was introduced into the lower Sacramento River in California. The species prospered along the Pacific coast and is now found from British Columbia south to Ensenada, Mexico (Forrester et al. 1972, Setzler et al. 1980). Striped bass also has been introduced into the Soviet Union, France, and Portugal (Doroshev 1970, Setzler et al. 1980).

Stock Decline and Restoration Activities

During the 1970s, there was a drastic reduction in the number of striped bass harvested by fishermen throughout its range along the eastern seaboard. In 1979, the US Congress passed an amendment to the Anadromous Fish Conservation Act (Public Law Number 96-118, 16 U.S.C. 757g) establishing the Emergency Striped Bass Study (ESBS) to examine the status of stocks, identify causes for decline in production, and perform an analysis of the economic impact of the decline in harvest (Chafee 1980). The Atlantic States Marine Fisheries Commission (ASMFC), as part of their Interstate Fishery Management Program (IFMP), created The Interstate Fisheries Management Plan for the Striped Bass (ASMFC 1981). Legislative action in 1984 created The Atlantic Striped Bass Conservation Act (Public Law Number 98-613); an amendment to the Act in 1986 (Public Law Number 99-432) authorized implementation of a Federal moratorium on striped bass fishing for those states failing to comply with the coastwide plan (USDOI

and USDOC 1987). Due to the large population of striped bass within the Roanoke River/Albemarle Sound and its economic importance, congressional monies were designated for study of this specific system to be administered by a North Carolina Striped Bass Study Management Board. This maturation and fecundity study is one of several studies funded by the Board to assess status of the stock and develop a strategy for stock restoration.

Spawning Characteristics

Striped bass is typically anadromous, spending a majority of its life in saltwater but migrating into freshwater or, in some instances, brackish water to spawn (Setzler et al. 1980). Populations from Albemarle Sound north to Nova Scotia are anadromous, while those south of Albemarle Sound to Florida and along the Gulf Coast to Louisiana are riverine and endemic (Rulifson et al. 1982). The spawning migration may be short, where local endemic populations may merely move upstream within the system to spawn, or it may comprise a rather lengthy trip covering hundreds of miles from offshore wintering grounds (Merriman 1941, Trent and Hassler 1968, Setzler et al. 1980).

In North Carolina, spawning striped bass populations exist within the Cape Fear River, Neuse River, Tar River, and Roanoke River/Albemarle Sound. The largest and only anadromous population spawns in the Roanoke River; spawning occurs from mid-April through early June downstream of the Roanoke Rapids Dam near Weldon, NC (Rulifson and Manooch 1990a). Hollis (1967) reported that older females from Chesapeake Bay are proportionally more prevalent on the spawning grounds early in the season while the young ones participate later (ASMFC 1981). However, communications with North Carolina Wildlife Resources Commission (NCWRC) and North Carolina Division of Marine Fisheries (NCDMF) personnel knowledgeable of Roanoke/Albemarle striped bass indicated that this pattern is not observed with Roanoke River spawning females.

Anthony Mullis (NCWRC), stated that younger female striped bass predominate the entire spawning season, but older females are more numerous later in the season. This observation was supported in conversations with Kent Nelson of the NCWRC, who also pointed out that medium size females (about 6-9 years of age) are more prevalent later in the season. Lynn Henry of the NCDMF agreed, and added that very few of the large females (10+ years old) are observed in any of the surveys.

As water temperatures rise, spawning is initiated. The optimal temperature range for spawning is 16-19°C (Hardy 1978, Rulifson and Manooch 1990b). Spawning by an individual female is thought to occur within a few hours (Lewis and Bonner 1966); however, little information is available on the number of eggs retained after spawning, and whether the percent of eggs retained within the ovaries correlates with size and age of the adult females.

A mature female is surrounded by up to 50 males as the eggs are broadcast into the surrounding water (Setzler et al. 1980). Males release sperm or "milt" close to the female as she rolls near the surface of the water. These "rock fights" are most prevalent at dusk and dawn (Setzler et al. 1980).

The number and size of eggs produced by an individual female is directly correlated with age and size of the female (Setzler et al. 1980, ASMFC 1981). Small, mature female striped bass do not produce as many eggs as older fish (Holland and Yelverton 1973). Monteleone and Houde (1990) studying fish collected from the Chesapeake Bay, noted that large females produce larger eggs and larger newly-hatched larvae (through the first 25 days of life) compared to those eggs and larvae produced by smaller mature females.

If natural larval mortality is in part size selective, then progeny from these large females should have a higher survival rate than those from smaller females. No field observations have been taken to support or refute this hypothesis; however, an attempt

was made to substantiate this claim through personal communication and review of the literature for spawning females in the Roanoke River. Field studies conducted by W. W. Hassler (North Carolina State University) from 1956-1987 (Manooch and Rulifson 1989), examined daily viability of striped bass eggs in the river during the major portion of the spawning season; no obvious seasonal trend in viability indicative of smaller or larger females spawning at different times throughout the season could be discerned. Egg viability is a function of environmental factors as well as maternal characteristics influenced by turbidity, water temperature and water velocity and other lesser known factors (Rulifson 1989). Personnel from the NCWRC familiar with the Roanoke/Albemarle striped bass population were contacted in an attempt to clarify this point. Robert Curry (Fisheries Management Coordinator) indicated that the Weldon, NC, hatchery utilizes medium-sized female striped bass in the 4.5 - 9.0 kg range, as low fecundity and poor hatching success resulted when smaller females were used. (Note: Larger females are not utilized primarily because of hatchery design and the relativly small number of larger females encountered.) Anthony Mullis and Kent Nelson added that hatching success is also influenced by: 1) injection of chorionic gonadotropin into the female to incite egg development, and 2) the stage of the eggs when stripped from the female.

Larvae are carried by the current into the lower Roanoke River and western Albemarle Sound (Rulifson et al. 1988). They may spend their first two years of life maturing in and around this nursery area (Hassler et al. 1981).

Female Maturation and Fecundity

The age at which female striped bass mature is an important consideration for developing harvest quotas and size limits of a fishery. If a population is depressed, a slot limit may allow more females to survive to first spawning, thereby increasing the number of eggs spawned each year. Previous investigations to determine maturation of female striped bass have resulted in maturity schedules that are quite variable. The wide range of differences in maturation may be manifestations of genetic information from different genotypes present within a population, due to use of different criteria in maturation studies, or a combination of these aspects (Specker et al. 1987). When data from all striped bass populations are combined, the resultant maturation schedule is wide ranging: 0 to 18% for age 3, 0 to 97% for age 4, and 17 to 100% for age 5 (Specker et al. 1987). Merriman (1941) estimated that all female stiped bass sampled off the Connecticut coast were mature by age 7. Lewis (1962) found that Roanoke/Albemarle females were all mature by age 5. Specker et al. (1987) determined that females collected offshore Rhode Island and Cat Cove, Massachusetts were all mature by age 7.

The objective of the study described herein was to determine a current maturity schedule for female striped bass in the Roanoke/Albemarle system and to estimate their potential and actual fecundity as functions of size and age. This study specifically compares results of the methodologies and criteria set forth for determining maturation by Merriman (1941), Lewis (1962) and Specker et al. (1987), each of which was applied to a single set of female Roanoke striped bass caught in 1989 and 1990. Results of this study will benefit fishery resource managers developing guidelines for future harvest quotas and other regulatory measures, as they work to restore striped bass populations in North Carolina and along the eastern seaboard.

METHODS

Field Data Collection

A total of 265 female striped bass were sampled from both commercial fishermen (n = 195) in Albemarle Sound and the lower Roanoke River, and recreational fishermen (n = 70) along the Roanoke River during the 1989 and 1990 spring spawning seasons (Table 1). Commercially caught fish were sampled on six occasions from Murray L. Nixon's Fishery, Inc. in Edenton, NC (89 in 1989; 71 in 1990), and three times from Evans Seafood in Greenville, NC (35 fish in 1989). (Those fish sampled at Evans Seafood were obtained from Murray Nixon's Fishery). These fish were caught by gill net in the lower Roanoke and western Albemarle Sound. Only fish being processed for shipment to the Midwest were allowed to be sampled. These fish were generally larger in size than those processed whole for local seafood markets.

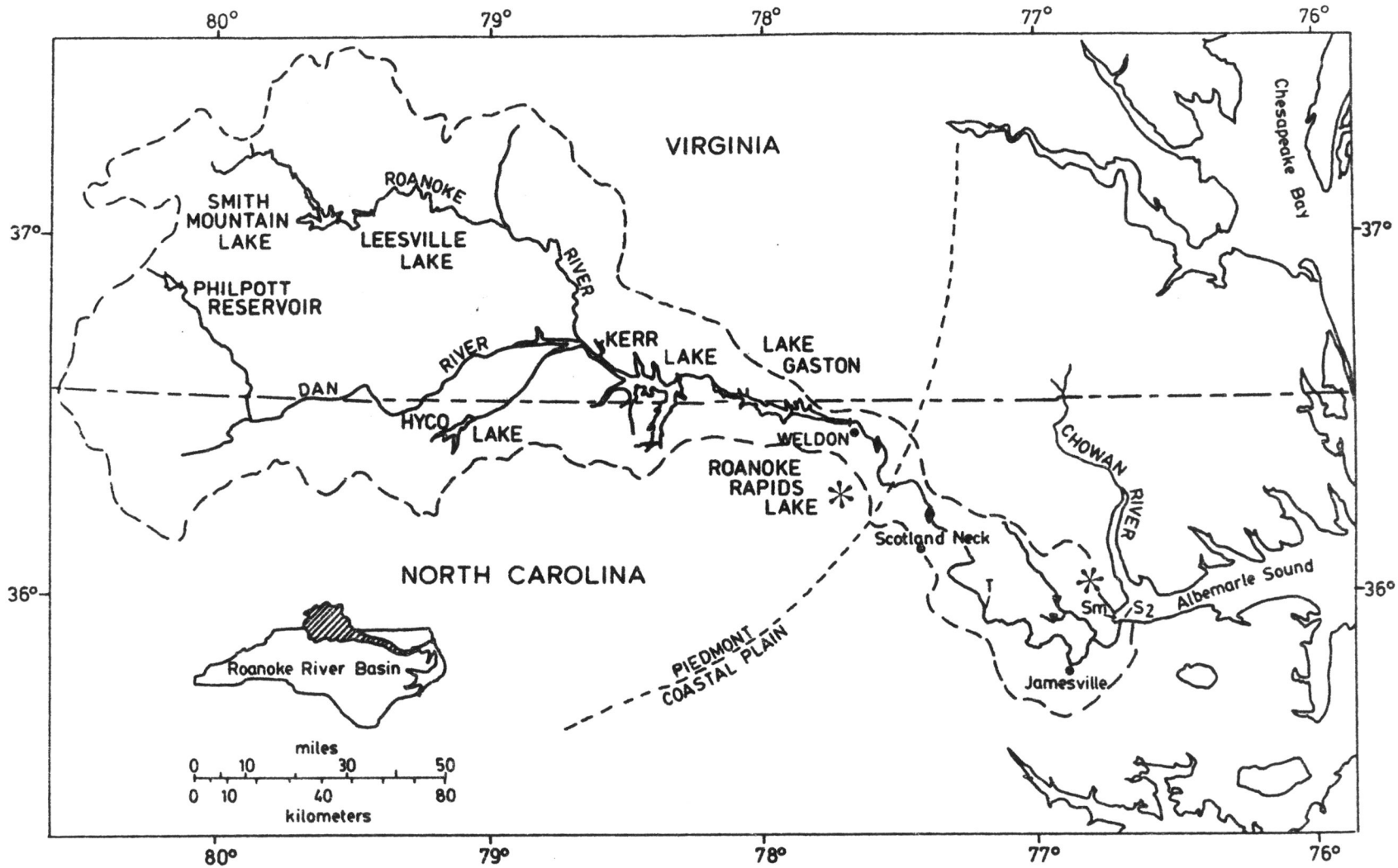
Female striped bass were sampled from the sport fishery near Weldon, NC, (Figure 1) during the annual creel survey conducted by the NCWRC (45 in 1989; 21 in 1990). Additional collections were made by the NCDMF (Albemarle Sound, n = 2) and from the Roanoke River at Barnhill's Landing (n = 2) in 1990.

In the field, fish were measured (mm) for total length (TL) (tip of snout to tip of pinched tail) and fork length (FL) (tip of snout to fork in tail). Total weight (kg) was measured with either a spring balance ($\pm$ 0.1 kg) or a hanging balance ($\pm$ 0.05 kg). For age analysis, scales were collected from above the lateral line in the mid-region of the body directly below the gap between the spinous and soft dorsal fins. Ovaries were surgically removed and placed on ice for return to the laboratory.

Table 1. Date and location of female striped bass sampled from the Roanoke River and Albemarle Sound in 1989 and 1990. Females sampled at Evans Seafood were obtained from Murray L. Nixon's Fishery, Inc. and those sampled from the NCDMF were sampled in the western Albemarle Sound. Weldon = River Mile (RM) 130; Barnhill's Landing = RM 117.

Date	Number of fish sampled	Commercial	Sport	Location
030389	4	X		Nixon
031489	1	X		Evans
031589	15	X		Evans
031789	19	X		Evans
032489	5	X		Nixon
033189	16	X		Nixon
041489	64	X		Nixon
050689	16		X	Weldon
052189	29		X	Weldon
040690	2			NCDMF
041390	1	X		Nixon
042090	70	X		Nixon
042790	4		X	Weldon
050390	7		X	Weldon
050690	2		X	Weldon
050890	2		X	Weldon
050990	6		X	Weldon
051390	2		X	Barnhill's
Total	265			

Figure 1. Roanoke River/Albemarle Sound system depicting the collection sites (*) for female striped bass in the spring of 1989 and 1990.


80°
79°
78°
77°
76°
37°
36°
VIRGINIA
NORTH CAROLINA
SMITH MOUNTAIN LAKE
ROANOKE
LEESVILLE LAKE
RIVER
PHILPOTT RESERVOIR
RIVER
KERR
LAKE
LAKE GASTON
DAN
HYCO
LAKE
WELDON
ROANOKE RAPIDS LAKE
Scotland Neck
CHOWAN RIVER
Albemarle Sound
Sm
S2
Jamesville
Chesapeake Bay
PIEDMONT
COASTAL PLAIN
Roanoke River Basin
miles
0 10 30 50
0 10 40 80
kilometers

Fecundity

Upon return to the laboratory, ovaries were visually examined for color and any peculiarities, weighed (± 0.01 g, Ainsworth-Model 200) and preserved. In most cases, the ovaries were frozen (-9°C). For 21 fish, two subsamples from each "fresh" ovary were removed, weighed individually, and placed in 10% formalin solution for fecundity analysis. The remaining portion was then enclosed in a Ziplock freezer bag and frozen for approximately six months.

For each fish, two subsamples of frozen ovarian tissue were removed from each ovary (n = 4), weighed individually, and placed in 10% formalin solution to preserve the eggs. After at least 24 hours, the samples were removed and individual eggs were counted under a dissecting microscope. The average number of eggs per gram of ovarian tissue was calculated for each fish using the equation

$$\text{Number of Eggs per Fish} = \frac{\frac{\Sigma E_i}{\Sigma w_i}}{n} \times W,$$

where: E_i = the number of eggs in each subsample,
w_i = the weight of each subsample,
n = the number of subsamples, and
W = the total ovarian weight

(Nielsen and Johnson 1983, Cailliet et al. 1986).

Regression analysis was performed to define the best determinant of fecundity using variables fish length (FL), total fish weight, and age.

To account for possible effects of dessication from prolonged freezing, fecundity was estimated for 21 fish where "fresh" ovarian samples were taken. These results were compared to those determined from subsamples taken from the same ovaries frozen for six months. Average fecundity was then estimated for each age class. Regression analy-

sis also was performed to determine if there was a statistical difference between the two methods.

A SAS program (SAS 1985) was utilized to calculate the F-statistic, comparing the fresh and frozen number of eggs per gram estimates. An F-statistic was then determined for the number of eggs per gram in relation to the age and weight of the female from which the ovaries were removed.

Maturity

A subsample of fresh ovarian tissue was removed from each fish and placed in Bouin's solution for histological examination to determine maturity. The tissue was considered "fixed" after a period of three days. After fixation, the Bouin's solution was decanted and replaced with 70% ethyl alcohol (ETOH) until the sample was blocked for sectioning (a minimum of 12 hours).

The fixed ovarian tissue was dehydrated in a graded series of alcohols and cleared in methyl salicylate prior to paraffin infiltration. The tissue was then blocked in paraffin. Serial sections (10 μm) using a rotary microtome were mounted on microscope slides and stained with hematoxylin and eosin.

Slides were projected onto a digitizing tablet (Jandel Inc. with Sigma-Scan software) and 100 oocytes from each fish were measured for length and width. A random numbers table was used to select 10 of the designated 16 numbered squares covering the digitizing tablet. For each of the 10 squares, 10 oocytes that had been sectioned through the nucleus were measured. In some instances, large oocytes filled the viewing area of the digitizing tablet and use of a random numbers table was not possible. In cases where there were only a few large oocytes, the largest oocytes were deliberately measured. Secondary growth characteristics indicative of oocyte maturity were recorded for each fish. These included opacity of the oocytes, presence or absence of small, clear-staining,

lipid vesicles within the cortex (cortical alveoli), and presence or absence of larger, dark-staining protein vesicles in the inner-mid cortex (vitellogenin) (Merriman 1941, Lewis 1962, Groman 1982, Specker et al. 1987, Mayer et al. 1988, Berlinsky and Specker 1991).

The average diameter of each oocyte was calculated by taking an average of its length and width. This diameter, along with any observed growth characteristics, was then compared to the criteria for maturation set forth by Merriman (1941), Lewis (1962), and Specker et al. (1987).

Age and Growth

Scales from each fish were utilized for age and growth determination. Scales were washed in warm water to remove any foreign material, mounted between two thin glass slides, dried, and viewed using a Microdesign microfiche reader at 24x and 60x magnification. Scales exhibiting a regenerated focus were eliminated from further consideration, while scales with a clear focus were examined and a representative individual chosen for annular measurements to the posterior edge. The focus, each annulus, and scale edge were recorded to the nearest millimeter.

Scale impressions onto acetate slides were made to verify the age of each fish determined from glass-mounted scales using the technique of multiple observations described by Kimura and Lyons (1991). If a discrepancy in aging occurred for a particular fish, the slides were examined again. In cases that could not be resolved, personnel from the NCDMF, Elizabeth City office examined the slides. If inconsistency remained, the scales were excluded from further analysis.

Back-calculations of fish length at age were performed utilizing the DISBCAL program (Frie 1982). The program requires the fish number, age, fork length at capture, magnification of the projected scale, and distance to each annuli and the scale edge.

DISBCAL contains two subprograms: REGRESS, which computes a least squares linear regression between fork length and scale radius; and BCAL, which back-calculates fork lengths to each annulus.

The REGRESS program calculates a body-scale constant from the linear regression of fork length against scale radius. This constant (A) is used in determining back-calculated length at age and is derived from the equation

$$L = (A) + B(S),$$

where,

L = fish length at capture,
S = scale radius,
A = body-scale constant, and
B = slope of the regression line.

The BCAL program was utilized to back-calculate fork length from the scale measurements using the Fraser-Lee formula

$$L_i = A + [(L_c - A) \times (S_i/S_c)],$$

where,

L_i = fork length at annulus i,
L_c = fork length at capture,
S_i = scale length to annulus i,
S_c = scale radius at capture, and
A = body-scale constant

(Ricker 1975, Frie 1982).

RESULTS

Fish were collected over similar time frames during 1989 and 1990 and samples for both years were combined for analysis. Season closures of the commercial and recreational fisheries limited our ability to sample the complete window of the spawning season; thus, possible significant differences in yearly or seasonal trends could not be considered valid.

Age and Growth

Back-calculations of fork length to age indicate that growth rate (length) is rapid during the first three years of life, and then decreases to a relatively slow rate as the fish reaches sexual maturity (Figure 2).

Female striped bass collected during March through May 1989 and April through May 1990 ranged in size from 344 to 1172 mm FL, averaging 540.9 $\pm$ 77.3 mm (n = 265). Weights ranged from 0.5 to 20.0 kg, averaging 2.5 $\pm$ 1.7 kg (n = 265). The length-frequency distribution (Figure 3) indicated a normal distribution with 88% of the fish falling between 450 and 600 mm FL. The weight-frequency distribution (Figure 4) produced a similar curve with a wide peak between 1500 and 3500 grams; 92.5% of all fish sampled fell into this range. Regression analysis indicated a highly significant linear length-weight relationship

Total fish weight = -6.381598 + 0.016316(Fork length)

(r^2 = 0.94, $p \leq 0.0001$, n = 265).

Approximately 95% (251 of 265) of the females were aged successfully. Initial counts of annular rings from scales pressed between two microscope slides agreed with counts from the acetate scale impressions in approximately 86% of the cases, with 12%

Figure 2. Growth patterns (FL in mm) of female striped bass from the Roanoke/Albemarle Sound system as estimated by back-calculation of scale annuli.

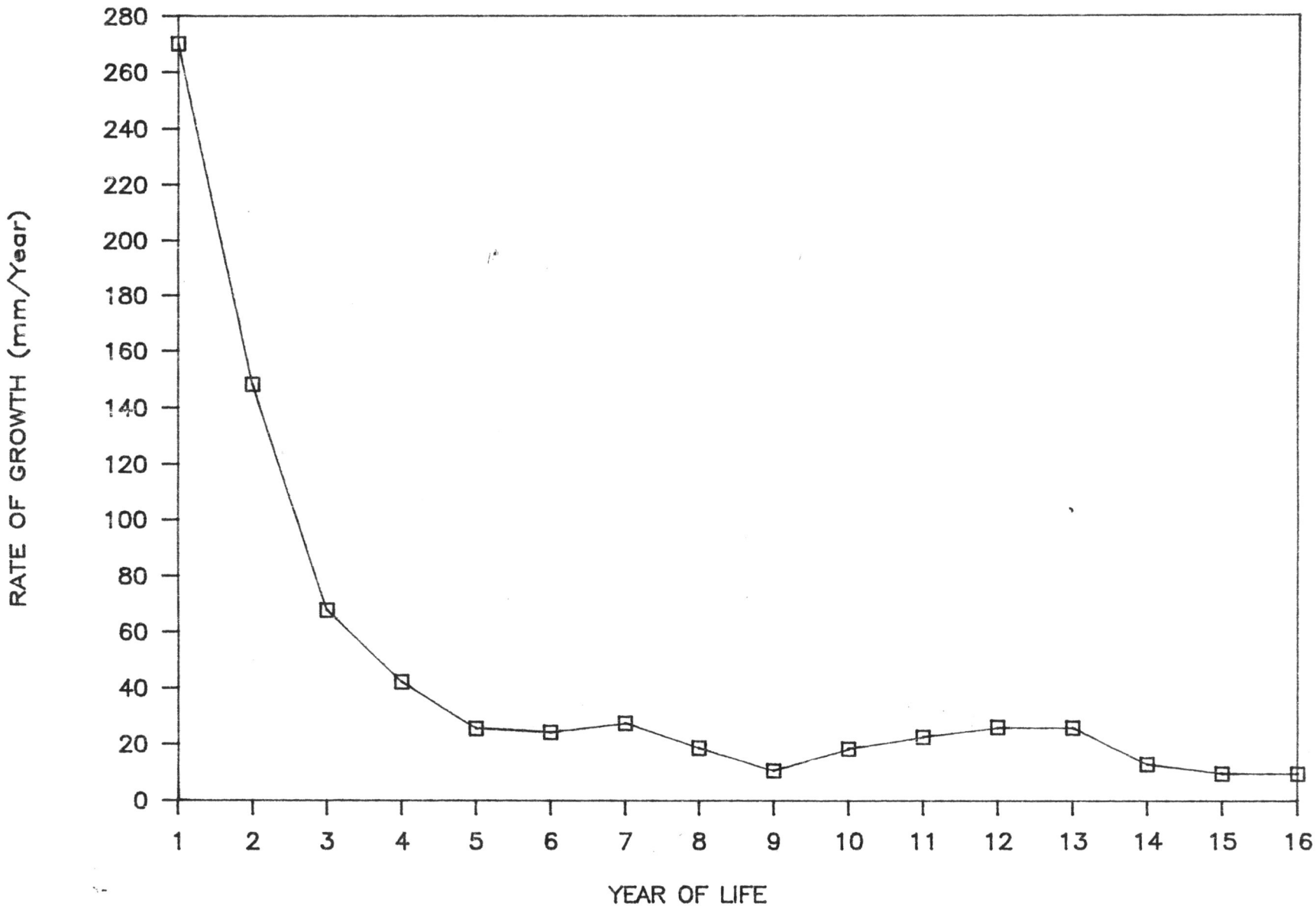

RATE OF GROWTH (mm/Year)
280
260
240
220
200
180
160
140
120
100
80
60
40
20
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
YEAR OF LIFE

Figure 3. Length frequency distribution (FL in 50-mm increments) of all female striped bass sampled from the Roanoke/Albemarle system in 1989 and 1990.

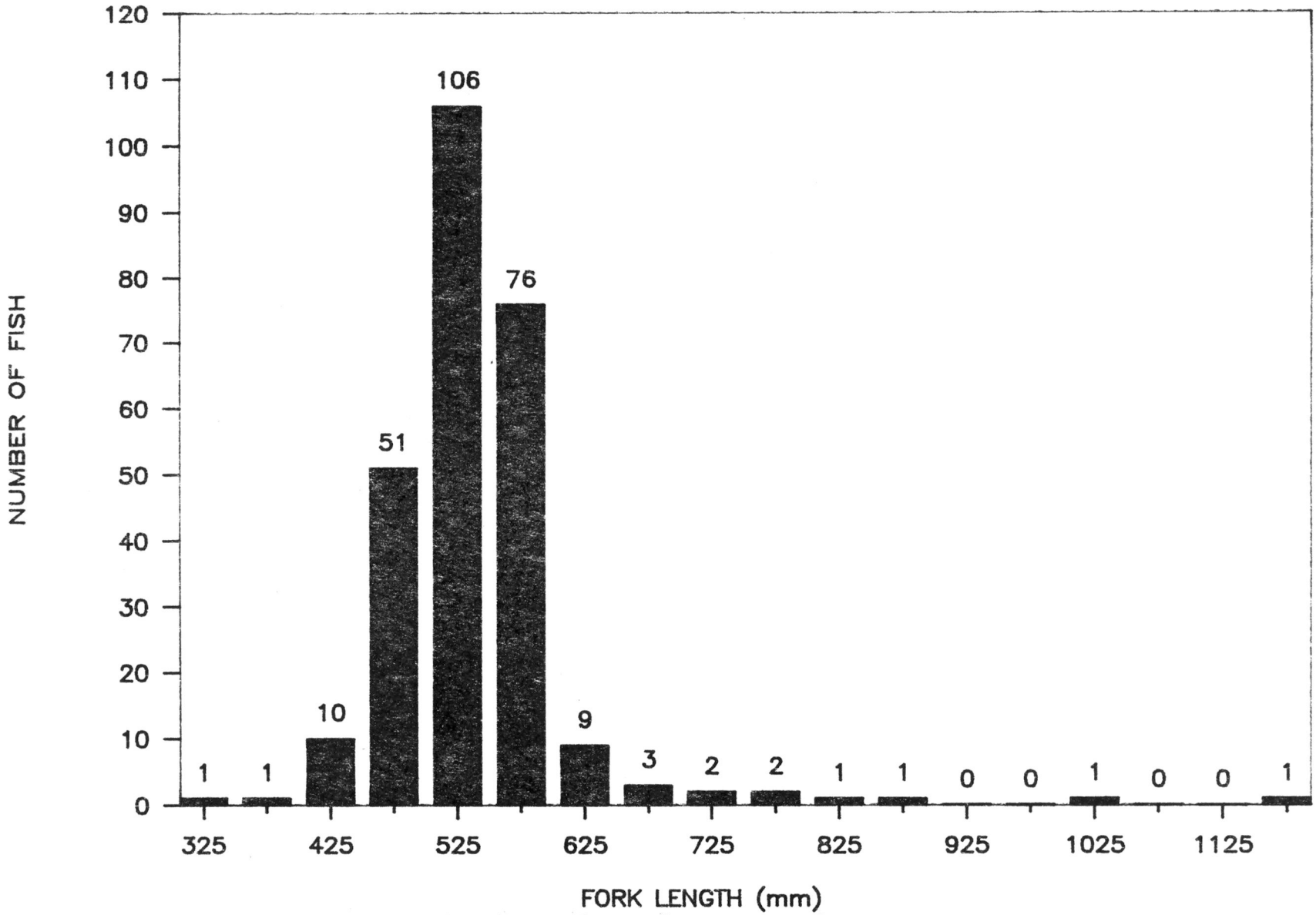
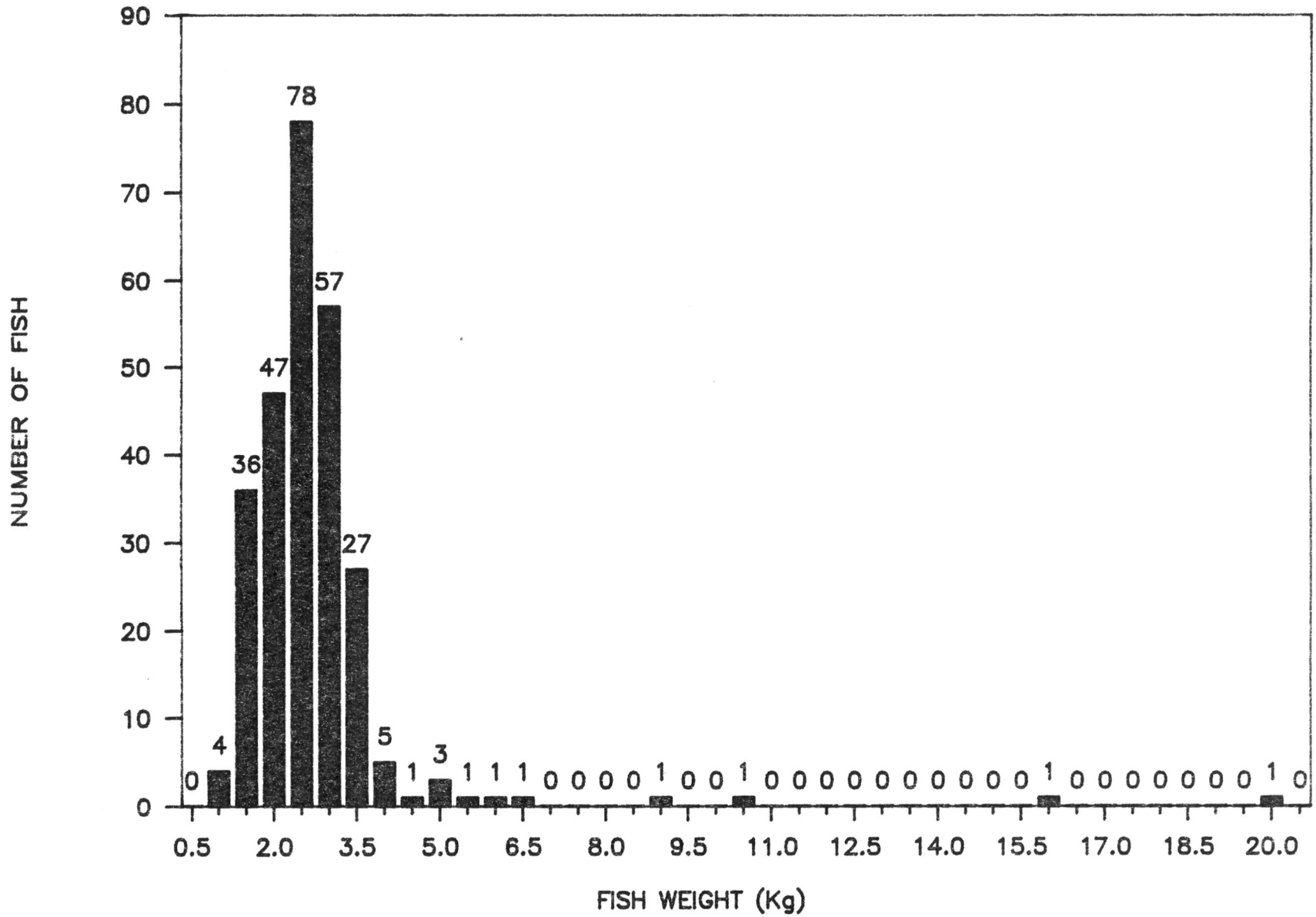

NUMBER OF FISH
120
110
100
90
80
70
60
50
40
30
20
10
0
1
1
10
51
106
76
9
3
2
2
1
1
0
0
1
0
0
1
325
425
525
625
725
825
925
1025
1125
FORK LENGTH (mm)

Figure 4. Weight frequency distrubution (0.5 kg increments) of all female striped bass sampled from the Roanoke/Albemarle system in 1989 and 1990.


NUMBER OF FISH
90
80
70
60
50
40
30
20
10
0
0 4 36 47 78 57 27 5 1 3 1 1 1 0 0 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0
0.5 2.0 3.5 5.0 6.5 8.0 9.5 11.0 12.5 14.0 15.5 17.0 18.5 20.0
FISH WEIGHT (Kg)

differing by one ring and the remaining 2% varying by 2 or more rings. Further review by NCDMF personnel resulted in all but 14 fish being aged successfully.

Fish ranged from age 2 to age 16 (Figure 5), with 88% (220 of 251) being age 3 through age 5. Of the 251 fish aged using this technique, back-calculation of fork lengths to previous ages was not possible on scales from four fish. This was due to the inability to locate a distinct focus; however, age was confidently established. The average fork length for each age class was calculated for the remaining 247 fish, presented in Table 2.

The DISBCAL program produced information regarding growth of each female. The DISBCAL plot of scale radius against fork length using the least-squares method resulted in the relationship:

$$FL = 165.1 + 56.8(\text{Scale radius}), (r^2 = 0.77, n = 247).$$

The body-scale constant (165.1) was then used to back-calculate fork length to age for each fish. These values were combined to determine an average back-calculated fork length for each age-class (Table 3). Average annual growth increments were calculated from these back-calculated lengths (Table 4).

Fecundity

Estimates of potential fecundity were determined using frozen ovarian tissue from a representative subsample of 62 fish. These fish ranged from age 3 through age 16 (Figure 6). Ovaries from the two age 2 fish sampled were found to be very small and threadlike, exhibiting no characteristics of maturation. These age 2 fish were considered immature and were not included in the analysis. Fish in age-classes 7 and older were intentionally sampled due to the low number of older fish collected. Gravimetric estimations of potential fecundity for each fish were projected and a mean fecundity estimate was determined for each age class (Figures 7 and 8).

Figure 5. Age frequency distribution of all female striped bass collected from the Roanoke/Albemarle system in 1989 and 1990.

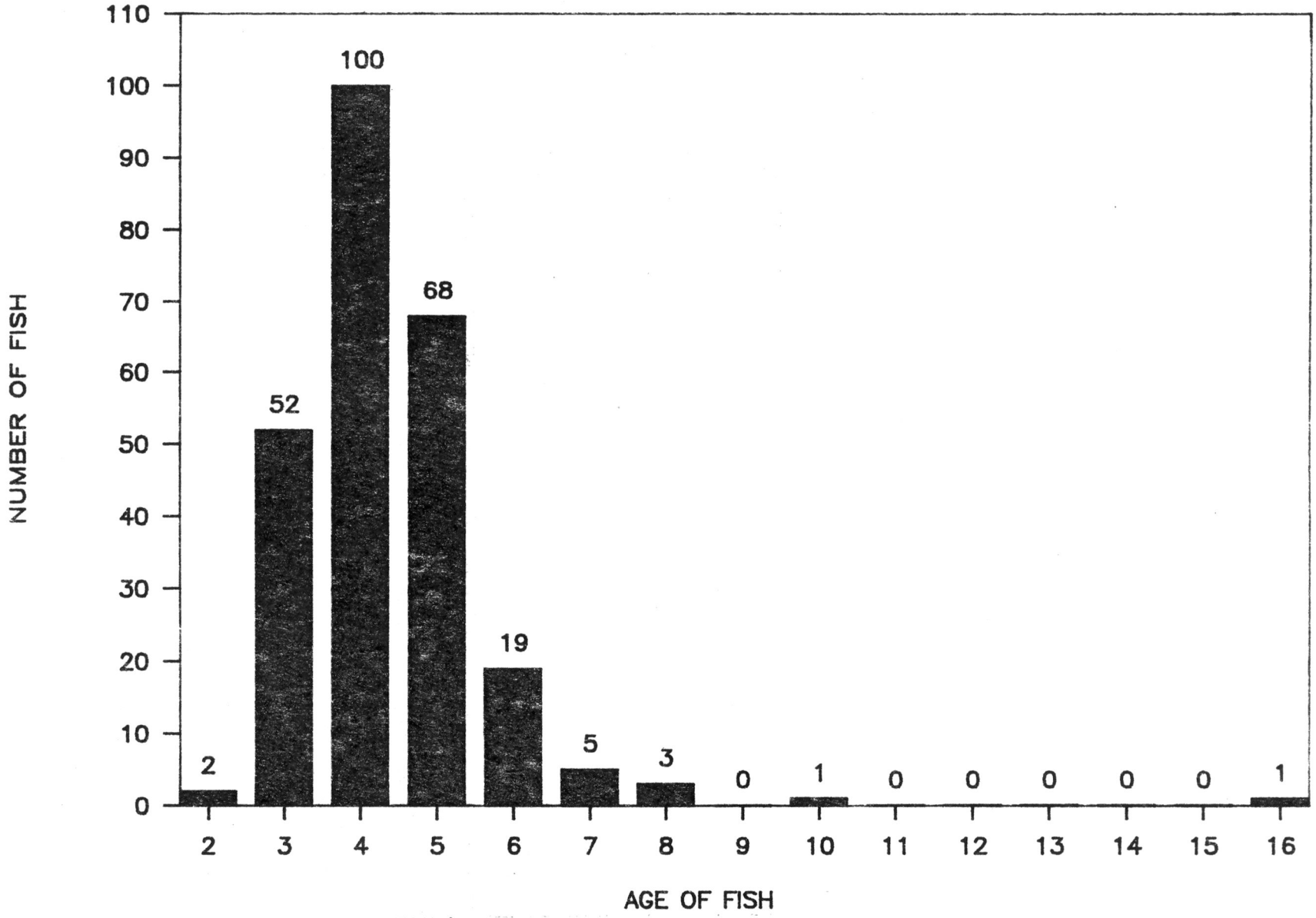

NUMBER OF FISH
110
100
90
80
70
60
50
40
30
20
10
0
2
52
100
68
19
5
3
0
1
0
0
0
0
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
AGE OF FISH

Table 2. Average length (FL, mm) and fish weight (kg) of striped bass at capture from the Roanoke/Albemarle system, North Carolina, in 1989-90 for each age class.

		Fork Length (mm)				Fish Weight (kg)			
Age	n	Average	Maximum	Minimum	S.E.	Average	Maximum	Minimum	S.E.
2	2	363	381	344	18.5	0.56	0.60	0.53	0.04
3	49	476	520	427	3.3	1.50	2.38	0.99	0.37
4	99	530	596	467	2.8	2.25	3.39	1.10	0.47
5	68	556	623	505	3.1	2.61	3.50	1.52	0.41
6	19	583	657	541	6.2	3.13	4.99	2.45	0.58
7	5	670	722	598	22.0	4.41	5.78	3.10	0.90
8	3	726	772	650	38.4	5.57	6.50	4.71	0.73
9	0								
10	1	815	815	815	--.-	8.52	8.52	8.52	-.--
11	0								
12	0								
13	0								
14	0								
15	0								
16	1	1172	1172	1172	--.-	20.00	20.00	20.00	-.--

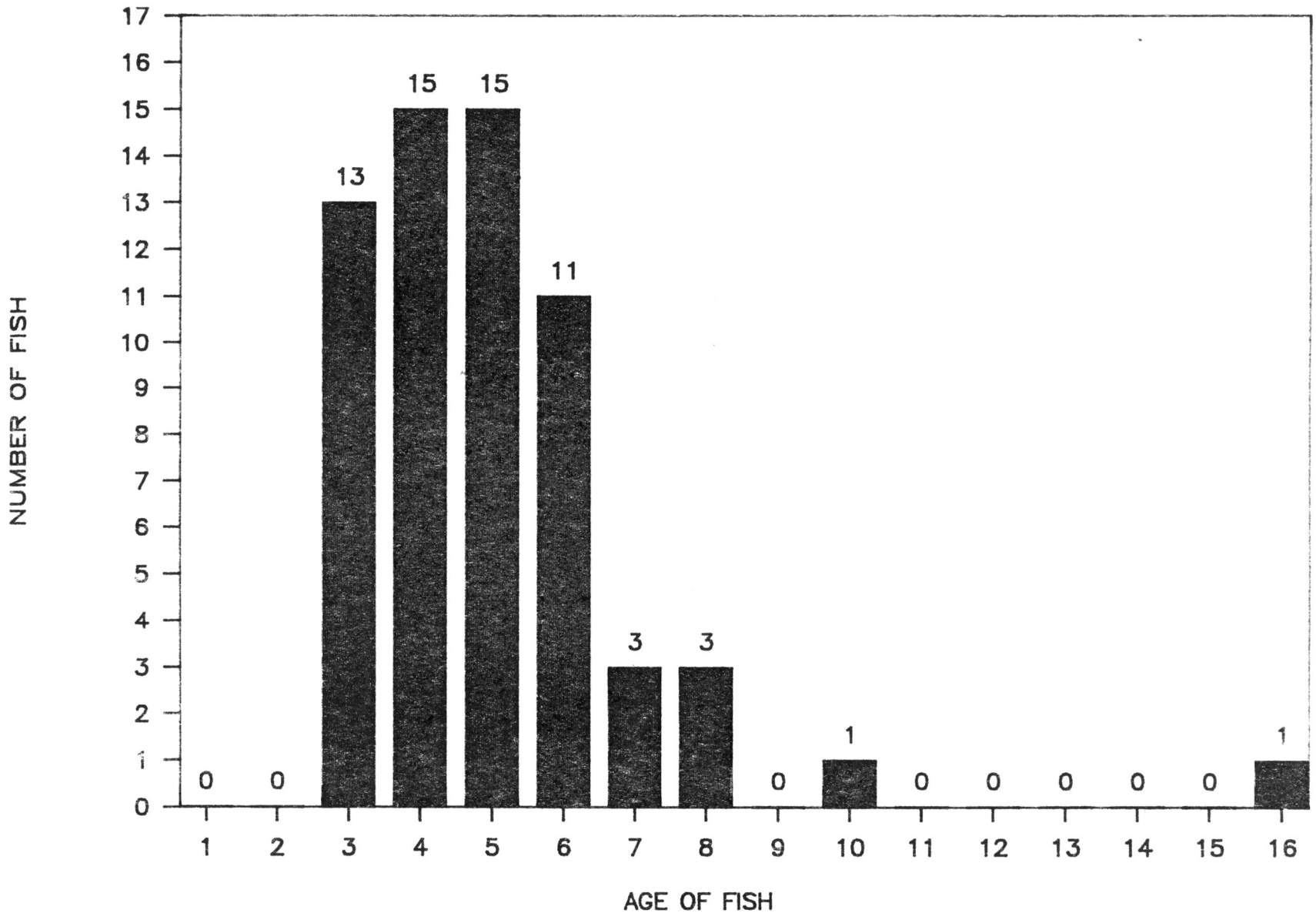
Table 3. Average back-calculated fork lengths (mm) for each age class of female Roanoke striped bass collected in 1989 and 1990.

Age	N	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	0	0.0															
2	2	259.5	362.5														
3	49	264.2	399.5	471.3													
4	99	269.7	416.5	480.6	525.5												
5	68	277.1	428.7	493.1	529.6	552.8											
6	19	265.2	428.2	495.5	534.6	560.6	580.3										
7	5	261.5	442.6	537.3	593.8	624.7	645.1	667.5									
8	3	272.6	440.4	569.4	631.9	658.9	689.6	710.9	722.8								
9	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0							
10	1	232.6	446.5	547.8	629.3	685.6	741.9	767.2	789.7	798.1	812.2						
11	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0					
12	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0				
13	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			
14	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
15	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
16	1	342.3	522.4	652.3	720.5	837.4	918.7	993.3	1,029.0	1,042.1	1,064.8	1,087.5	1,113.5	1,139.5	1,152.5	1,162.3	1,172.0
All		270.1	418.3	486.6	532.7	565.7	618.7	723.1	797.4	920.1	938.5	1,087.5	1,113.5	1,139.5	1,152.5	1,162.3	1,172.0
N		247	247	247	245	196	97	29	10	5	2	2	1	1	1	1	1
Std Err		1.83	1.88	1.95	2.50	4.86	14.67	35.02	63.09	121.97	126.33	0.00	0.00	0.00	0.00	0.00	0.00

Table 4. Average annual increments of back-calculated fork lengths (mm) for each age class of female Roanoke striped bass collected in 1989 and 1990.

Age	N	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	0	0.0															
2	2	259.5	103.0														
3	49	264.2	135.3	71.8													
4	99	269.7	146.8	64.1	44.9												
5	68	277.1	151.5	64.5	36.5	23.2											
6	19	265.2	163.0	67.3	39.1	26.0	19.7										
7	5	261.5	181.2	94.7	56.4	31.0	20.4	22.4									
8	3	272.6	167.8	129.0	62.5	27.0	30.7	21.3	11.8								
9	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0							
10	1	232.6	213.8	101.3	81.6	56.3	56.3	25.3	22.5	8.4	14.0						
11	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0					
12	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0				
13	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			
14	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
15	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
16	1	342.3	198.1	129.9	68.2	116.9	81.2	74.7	35.7	13.0	22.8	22.7	26.0	26.0	13.0	9.7	9.7
All		270.1	148.2	67.8	42.3	25.6	24.2	27.6	18.7	10.7	18.4	22.7	26.0	26.0	13.0	9.7	9.7
N		247	247	247	245	196	97	29	10	5	2	2	1	1	1	1	1
Std Err		1.83	1.53	1.49	1.18	1.49	2.75	6.05	4.87	2.29	4.36	0.00	0.00	0.00	0.00	0.00	0.00

Figure 6. Age frequency distribution of all female striped bass used for the fecundity analysis.


NUMBER OF FISH
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
0
0
13
15
15
11
3
3
0
1
0
0
0
0
0
1
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
AGE OF FISH

Female striped bass produced approximately an additional 100,000-200,000 eggs with each year of growth; however, this yearly increase is somewhat variable and not linear. The average potential fecundity for an age 3 female possessing maturing eggs was about 181,000 (n = 13). Potential fecundity ranged up to approximately 5,000,000 eggs for a single age 16 female.

All possible regression analyses were performed to define the best determinant of fecundity. Regression analysis of fecundity against fish length (FL) and weight was similar; as the r^2 values were 0.82 and 0.83, respectively. The r^2 values did not increase significantly when covariates were included. Further analysis was then performed using fecundity against fish weight, length, and age; the single age 10 and age 16 fish were not included so as to reduce bias caused by singular data.

Regression analysis of fecundity as a function of total fish weight was performed on the remaining 60 fish. Cook's D influence statistic (SAS 1985) for each fish indicated that three fish were at least two standard deviations from the mean. These fish were removed from the total fish weight analysis. Regression analysis of the remaining 57 fish was performed again, resulting in the relationship

$$\begin{matrix}\text{Number of} \\ \text{eggs produced} \\ \text{per fish}\end{matrix} = -109163.3 + 228608.3(\text{Total fish weight}).$$

Results of analysis of variance (ANOVA) indicated that total fish weight was a good predictor of potential fecundity ($r^2 = 0.83$, $p \leq 0.0001$). The calculated potential fecundity for an age 3 female (based on total fish weight) was estimated at 245,000 eggs.

Cook's D influence statistic was calculated, relating fecundity as a function of fork length. This resulted in three fish at least two standard deviations from the mean.

Figure 7. Estimated potential fecundity of female Roanoke/Albemarle striped bass collected in 1989 and 1990.

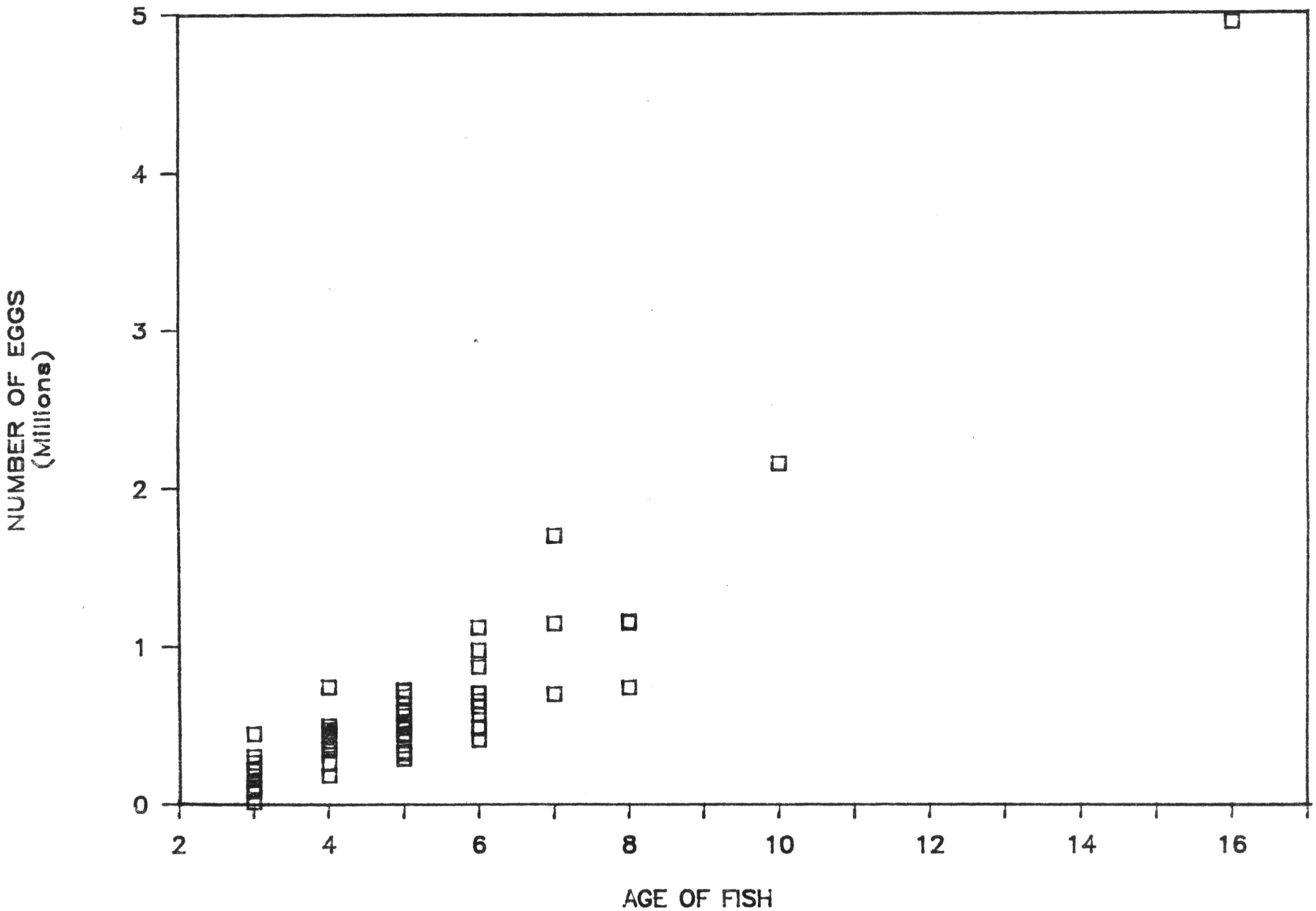
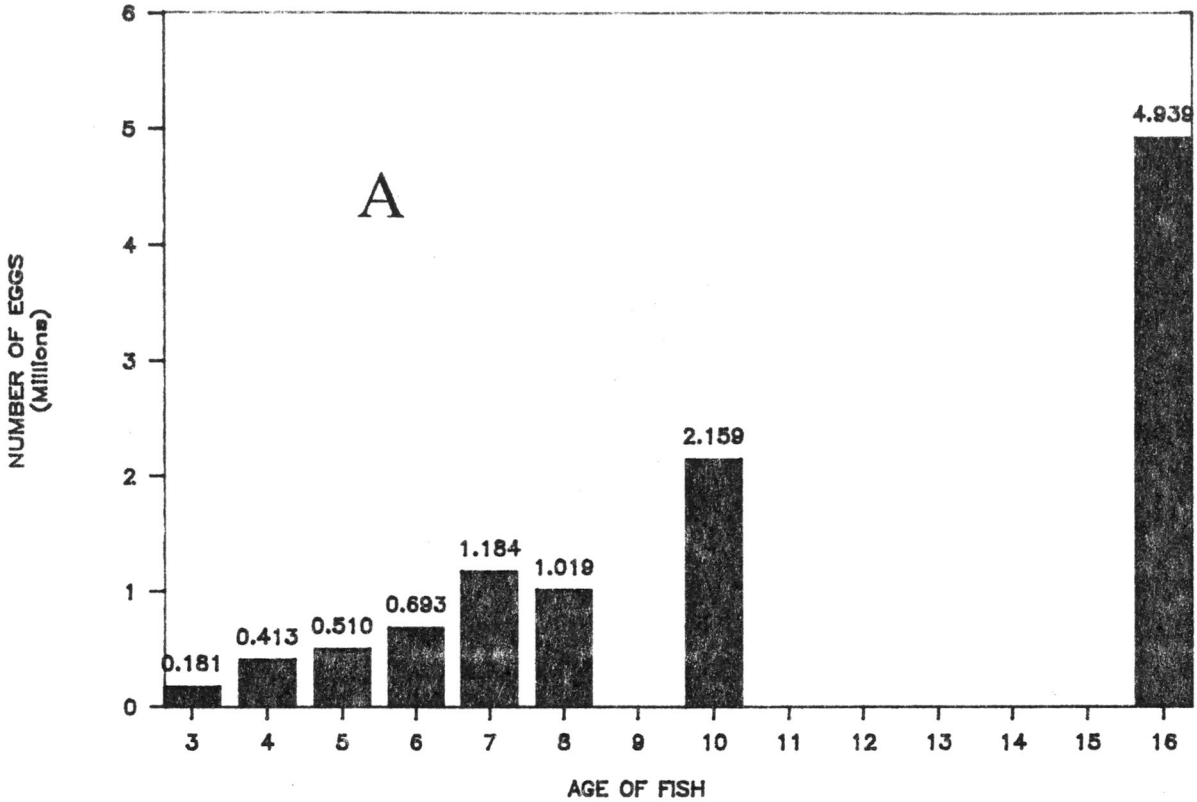
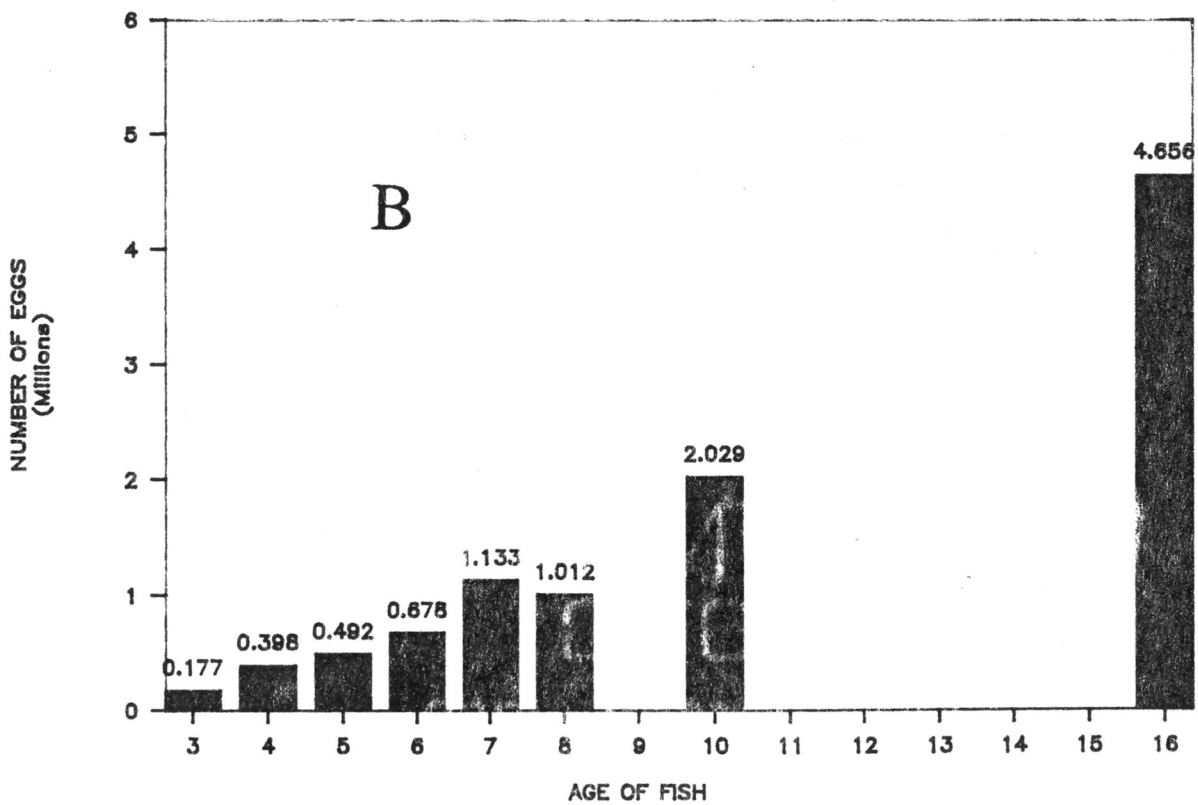

NUMBER OF EGGS
(Millions)
0
1
2
3
4
5
2
4
6
8
10
12
14
16
AGE OF FISH

Figure 8. Estimated average number of eggs produced by female Roanoke/Albemarle striped bass collected in 1989 and 1990. A) Fecundity estimates (frozen); B) fecundity estimates (adjusted).


A
NUMBER OF EGGS (Millions)
AGE OF FISH
0.181
0.413
0.510
0.693
1.184
1.019
2.159
4.939
0
1
2
3
4
5
6
3
4
5
6
7
8
9
10
11
12
13
14
15
16


B
NUMBER OF EGGS (Millions)
AGE OF FISH
0.177
0.398
0.492
0.678
1.133
1.012
2.029
4.656
0
1
2
3
4
5
6
3
4
5
6
7
8
9
10
11
12
13
14
15
16

Upon removing these three fish from the fork length analysis, regression analysis of the remaining 57 fish resulted in the relationship

$$\text{Number of eggs produced per fish} = -1553051.5 + 3696.8(\text{Fork length}).$$

The ANOVA relationship of fecundity as a function of fork length was very similar to the same analysis using total fish weight ($r^2 = 0.82$, $p \leq 0.0001$). The calculated fecundity estimate (based upon the average fork length of an age 3 fish) was approximately 211,000 eggs.

Regression analysis of fecundity as a function of age, and the resultant Cooks D influence statistic, indicated that three fish were at least two standard deviations from the mean and were subsequently removed from the analysis. Regression analysis of the remaining 57 fish was performed again, resulting in the relationship

$$\text{Number of eggs produced per fish} = -315973.7 + 168567.6(\text{Fish age}).$$

Regression analysis indicated that potential fecundity was significantly correlated with fish age, but less so than with total fish weight ($r^2 = 0.70$, $p \leq 0.0001$). The average number of eggs for an age 3 female by this method was slightly less than 196,000 eggs.

Estimates of potential fecundity from fresh and frozen ovarian tissue were significantly different ($F = 4.99$, $p = 0.0412$). The magnitude of the effect was significantly correlated with age of the fish ($F = 3.53$, $p = 0.0263$); thus, the error in estimation increased with increasing fish age. In other words, use of fresh ovarian tissue is more accurate, as use of frozen ovarian tissue may result in overestimation of fecundity, especially with increasing fish age. A frozen→fresh adjustment formula was determined to

compensate for effects of dessication on the frozen tissue

$$\text{Estimated number of eggs per gram of fresh ovarian tissue} = 164.67 + 0.88(\text{Frozen eggs per gram}).$$

Adjusted fecundity estimates were calculated for each age class and compared to previously determined fecundity estimates in Table 5.

Maturity

Ovarian sections from 214 female striped bass ranging from age 2 through age 10 were observed for indications of maturity. Many of the oocytes were asymmetrical, so for each the length and width were averaged to determine an average oocyte diameter. For each fish, the resultant 100 oocyte diameters were compared to minimum diameter specifications for maturity set forth by Merriman (1941) of 0.216 mm, Lewis (1962) of 0.16 mm, and Specker et al. (1987) of 0.15 mm. Other maturation criteria such as the presence or absence of cortical alveoli and vitellogenin, and in some cases the opacity of oocytes within the ovary, were recorded subjectively on a per fish basis. Mature and immature ova were distinguished using ovum diameter measurements as well as presence or absence of the previously mentioned criteria. For each study, if the previous investigator(s) found the presence of oocytes that met the minimum diameter criteria and showed signs of secondary development, the fish was considered mature. However, the present study considered these fish to be maturing, but not necessarily mature (i.e., releasing viable eggs during the imminent spawning season). To estimate those maturing fish in a prespawning condition, a conservative approach implementing a cutoff of 10% of the oocytes meeting the required minimum diameter was used to compare the three studies. Using this approach, the resultant maturity schedules were very similar and uniform (Figure 9), but lower than those determined using the single oocyte criterion. The matu-

Table 5. Relationship of estimated potential fecundity, calculated by age, total fish weight, and fork length (FL, mm), for female striped bass of the Roanoke/ Albemarle system.

		Frozen tissue				Adjusted frozen tissue
Age	n	Estimated Fecundity	Calculated (by weight)	Calculated (by FL)	Calculated (by age)	[a]Estimated fecundity
3	13	180,929	245,212	211,007	195,558	177,130
4	15	413,440	412,984	416,920	364,532	397,729
5	15	509,817	494,768	511,302	533,477	492,168
6	10	693,130	612,693	620,232	702,422	677,604
7	3	1,184,410	901,087	931,840	871,366	1,012,016
8	3	1,018,675	1,164,059	1,138,416	1,040,311	1,133,463
9						
10	1	2,158,868	1,830,527	1,464,718	1,378,200	2,028,787
.						
.						
.						
16	1	4,938,991	4,424,102	2,778,514	2,391,869	4,656,338

[a]Utilizing frozen→fresh correction formula to adjust for error associated with freezing.

ration schedule using the 10% cutoff was: age 3 females, 45%; age 4 females, 94%; age 5 females, 95%; and for age 6 females, 100%. Analysis was repeated using the minimum percentage of mature oocyte criterion at the 20%, 30%, and 40% levels. Utilization of the 10%, 20%, and 30% mature oocyte criteria resulted in similar schedules among the methods. Using the 20% mature oocyte criterion, the maturation schedule was: age 3 females, 43%; age 4 females, 93%; age 5 females, 95%; and 100% for all age 6 females. The maturation schedule using the 30% mature oocyte criterion was: age 3 females, 37%; age 4 females, 92%; age 5 females, 92%; and 100% for all age 6 females. These results were similar in that all Roanoke females were mature by age 6 (Figures 10 and 11). The maturity schedule calculated from a 40% cutoff resulted in 80% maturity or less through age 8. Using the 40% minimum oocyte criterion, the maturation schedule was: age 3 females, 22%; age 4 females, 67%; age 5 females, 71%; age 6 females, 75%; age 7 females, 80%; age 8 females, 67%; and 100% mature at age 10 (Figure 12).

Figure 9. A comparison of the age to maturity of female Roanoke striped bass determined by three methods (Merriman 1941, Lewis 1962, and Specker et al. 1987) using a 10% mature oocyte criterion.

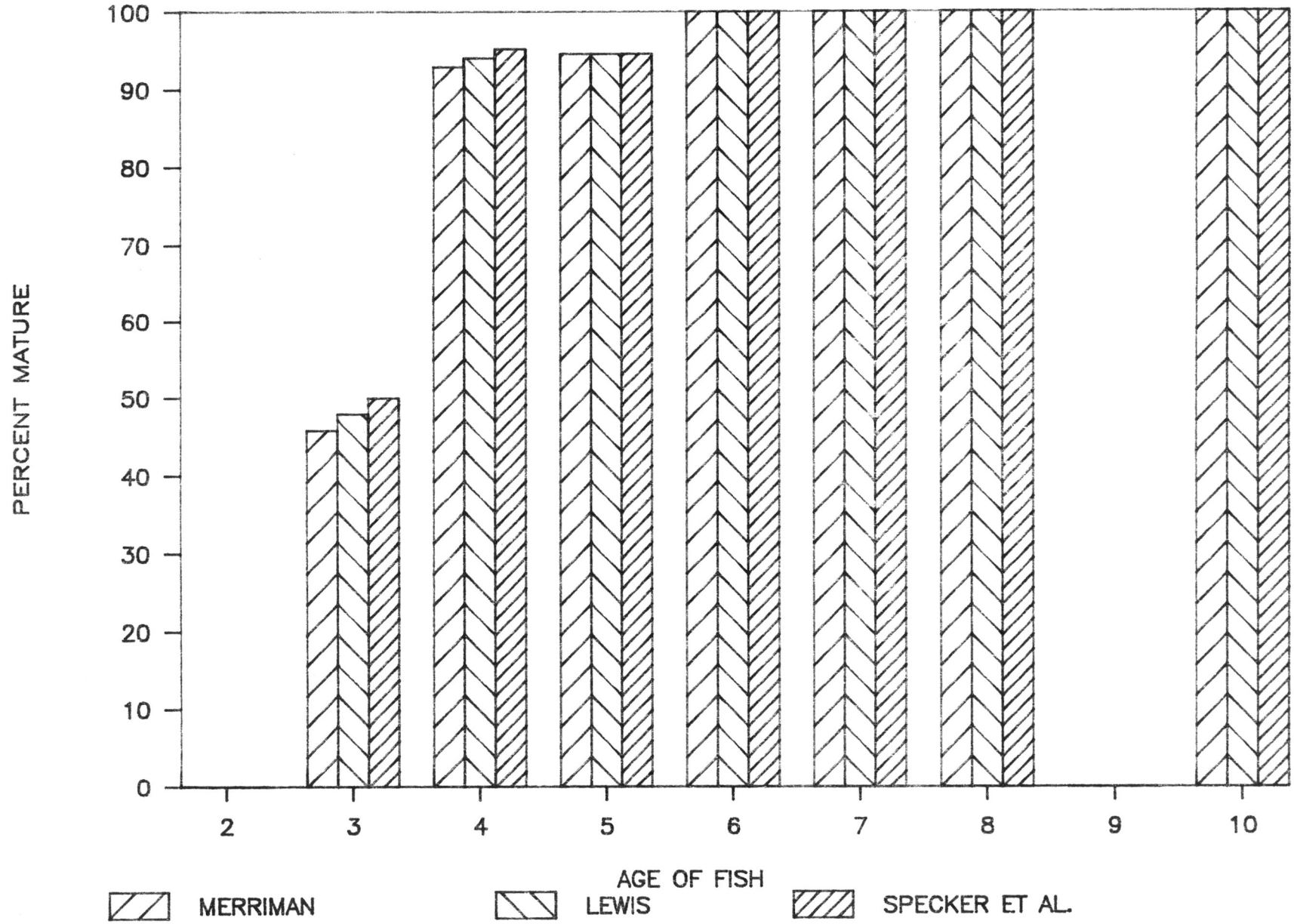

PERCENT MATURE
100
90
80
70
60
50
40
30
20
10
0
2
3
4
5
6
7
8
9
10
AGE OF FISH
MERRIMAN
LEWIS
SPECKER ET AL.

Figure 10. A comparison of the age to maturity of female Roanoke striped bass determined by three methods (Merriman 1941, Lewis 1962, and Specker et al. 1987) using a 20% mature oocyte criterion.

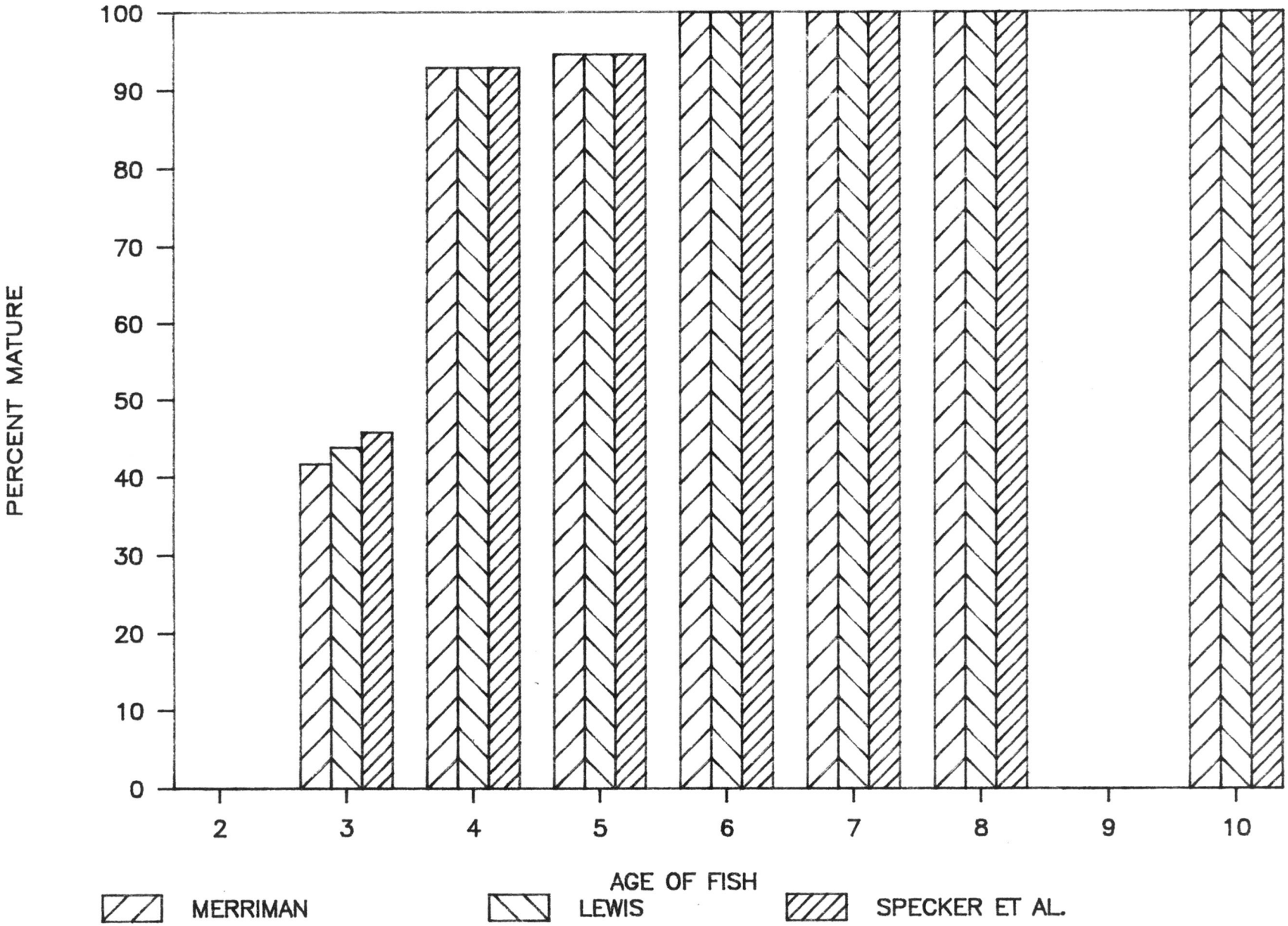

PERCENT MATURE
100
90
80
70
60
50
40
30
20
10
0
2
3
4
5
6
7
8
9
10
AGE OF FISH
MERRIMAN
LEWIS
SPECKER ET AL.

Figure 11. A comparison of the age to maturity of female Roanoke striped bass determined by three methods (Merriman 1941, Lewis 1962, and Specker et al. 1987) using a 30% mature oocyte criterion.

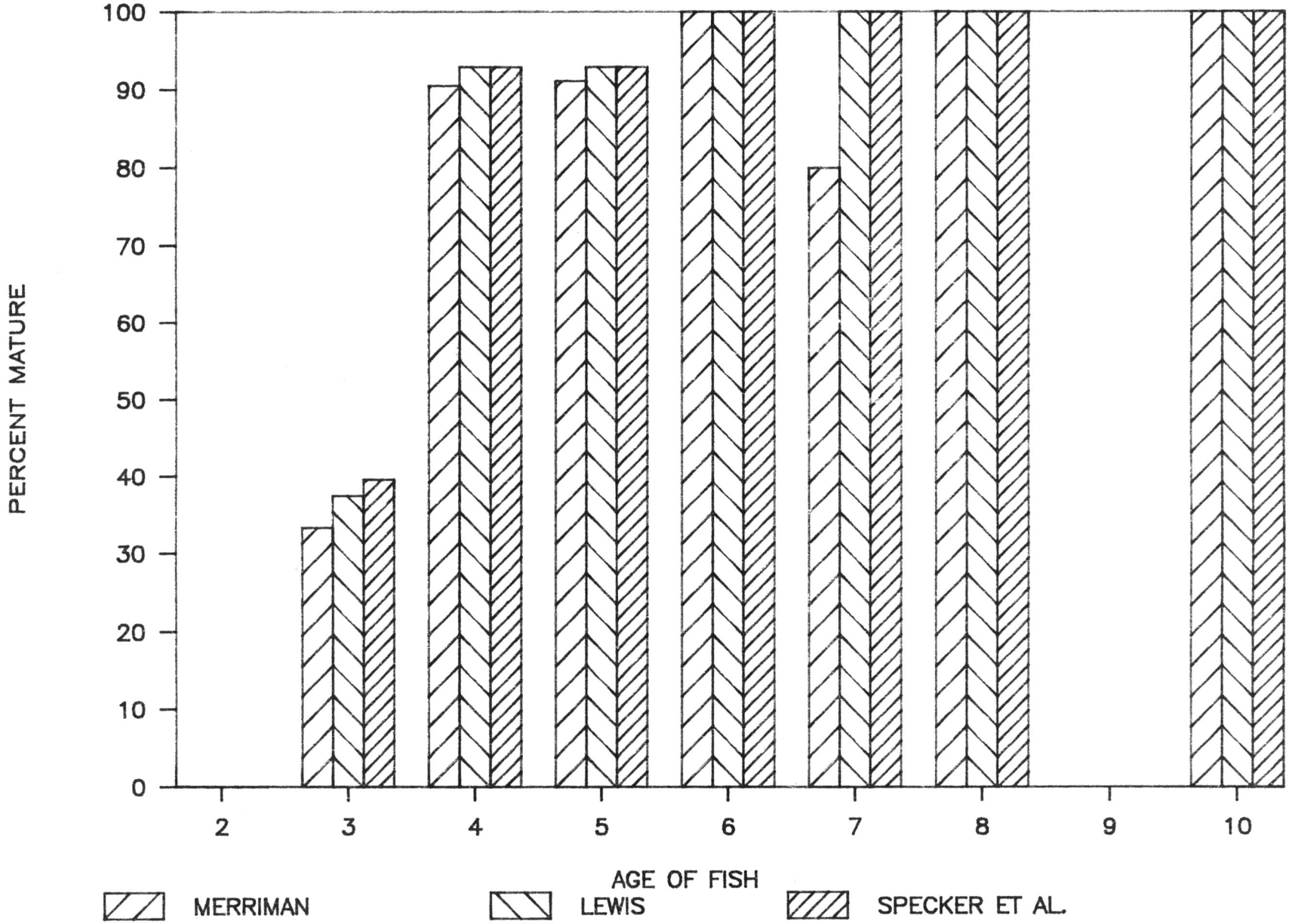
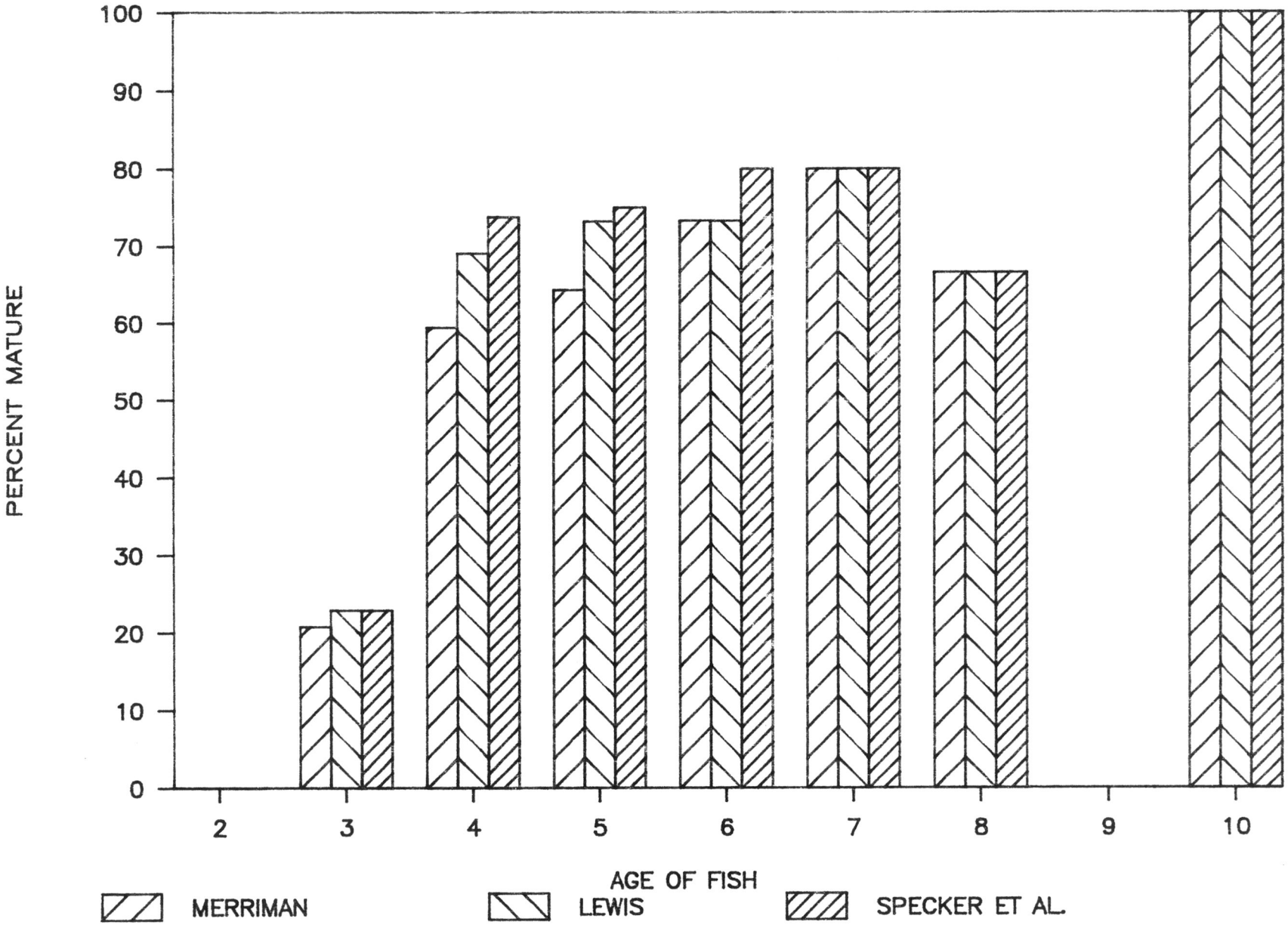

PERCENT MATURE
100
90
80
70
60
50
40
30
20
10
0
2
3
4
5
6
7
8
9
10
AGE OF FISH
MERRIMAN
LEWIS
SPECKER ET AL.

Figure 12. A comparison of the age to maturity of female Roanoke striped bass determined by three methods (Merriman 1941, Lewis 1962, and Specker et al. 1987) using a 40% mature oocyte criterion.


PERCENT MATURE
100
90
80
70
60
50
40
30
20
10
0
2
3
4
5
6
7
8
9
10
AGE OF FISH
MERRIMAN
LEWIS
SPECKER ET AL.

DISCUSSION

Fish were sampled from commercial and sport catches along the Roanoke/Albemarle during the spring spawning seasons of 1989 and 1990. As with any sampling scheme of this type, there is a bias in the size and related age structure of the sampled fish. Fisherman preference as well as observation of minimum size restrictions for recreational fishermen possibly introduced a size selectivity bias for those fish close in size to the regulations. In other words, the largest age 3 fish may have been retained but the smallest age 3 fish released. Also, it was possible to sample only the larger commercially-caught fish, which were being prepared for shipment to the Midwest. From our age and size distributions, it appears that fish from age 3 through age 5, of fork lengths from 450 to 600 mm, were most likely to be sampled using these methods. This may have excluded a portion of the smallest age 3 or age 4 fish and all of the age 2 fish. However, both age 2 fish examined exhibited no signs of maturation. Average fork length values by age were similar to those values determined in previous studies by Trent and Hassler (1968) and Harriss et al. (1985). This indicates that sampling bias was comparable to these previous studies. Without examining every individual within a population, it is impossible to determine actual sampling bias.

Age and Growth

Delineation of annular rings was relatively easy for young fish and progressively more difficult with increasing fish age. It is generally assumed that formation of a true annulus is caused by the slowing down or cessation of growth in the winter; however, these rings are not noticeable till late spring (Merriman 1941). Decrease in annual scale growth with age causes a crowding of annuli near the scale edge. The inclusion of false ages should have been minimized by the large number of young fish sampled, the scale

verification technique, and multiple scale readings as described by Kimura and Lyons (1991).

Fecundity

Fecundity estimates for all age classes were similar to those conducted on Roanoke/Albemarle striped bass by Lewis and Bonner (1966), and on striped bass of unknown origin collected offshore North Carolina by Holland and Yelverton (1973) (Table 6). Fecundity estimates determined for each of the previous studies were derived from formalin preserved ovaries, while fecundity estimates for this study were obtained from frozen tissue; however, use of a frozen→fresh adjustment formula would have brought these values in line with fecundity estimates determined from fresh tissue.

In the present study, the comparison between fresh and frozen ovarian samples taken from the same fish resulted in a statistically significant difference in fecundity. Frozen ovarian tissue resulted in statistically higher fecundity estimates for females over age 4, which increased with fish age (Figure 13). This may possibly overestimate the actual potential fecundity for those specific ages. An anomaly occurred for age 8 females, in that the eggs per gram decreased. This may have been an artifact of the small sample size or an early release of eggs prior to the spawning act. The error associated with comparing fresh and frozen ovarian tissue for fecundity analysis was statistically significant for the overall sample ($F = 4.99$, $p \leq 0.0412$) and was a function of age-class ($F = 3.53$, $p \leq 0.0263$). This may be a direct result of ovarian dessication in older females. These larger eggs may fracture more easily when frozen because of their liquid content.

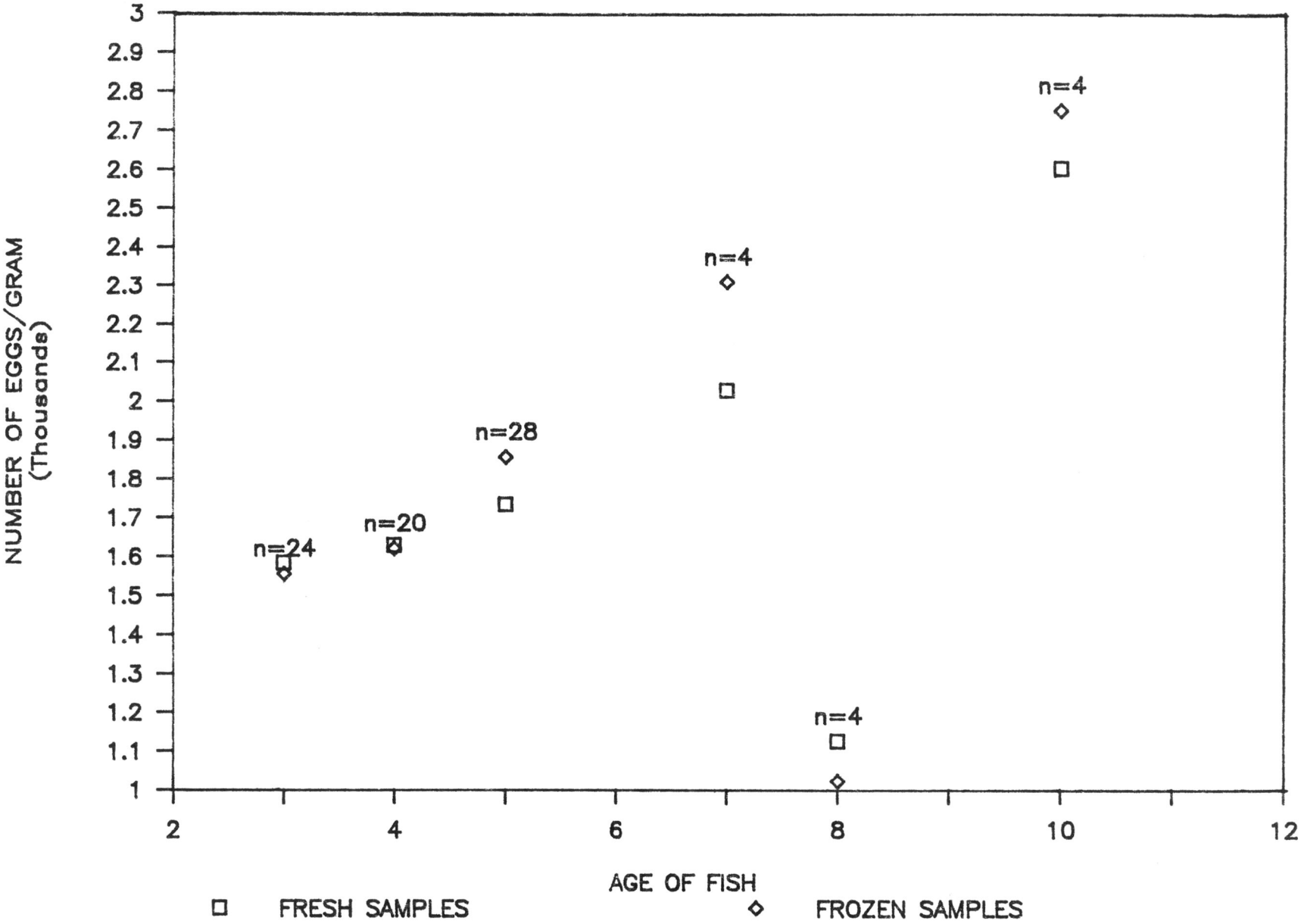
Egg fragments were present in most of the frozen samples observed, resulting in increased work-up time to discern individual eggs, and may have caused some error in the individual egg counts. Samples from fresh ovarian tissue were much quicker to

Table 6. Estimated fecundity of female Roanoke striped bass compared to previous investigations. Number of fish examined in parentheses.

Age	Lewis and Bonner (1966)	[a]Holland and Yelverton (1973)	Present study	
			Frozen[b]	Frozen (Adjusted)[c]
3			180,929	177,130 (13)
4	345,794 (63)		413,440	397,729 (15)
5	438,667 (15)		509,817	492,168 (15)
6	615,556 (9)		693,130	677,604 (11)
7	752,059 (17)	614,243 (1)	1,184,410	1,012,016 (3)
8	820,500 (14)	1,703,200 (4)	1,018,675	1,133,463 (3)
9	909,545 (11)	2,099,811 (13)		
10	910,167 (6)	2,991,733 (4)	2,158,868	2,028,787 (1)
11		2,928,498 (10)		
12		3,407,767 (2)		
13		3,391,002 (1)		
.				
.				
16			4,938,991	4,656,338 (1)
Total examined	135	35		62

[a]Holland and Yelverton caught these fish offshore North Carolina.
[b]Present study used frozen tissue when determining fecundity estimates.
[c]Fecundity values associated with frozen→fresh adjustment formula.

Figure 13. Differences in the number of striped bass eggs per gram of ovarian tissue determined by examination of fresh and frozen ovaries.


NUMBER OF EGGS/GRAM
(Thousands)
3
2.9
2.8
2.7
2.6
2.5
2.4
2.3
2.2
2.1
2
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1
n=24
n=20
n=28
n=4
n=4
n=4
2
4
6
8
10
12
AGE OF FISH
FRESH SAMPLES
FROZEN SAMPLES

process because the eggs were almost exclusively whole. This information indicates that fecundity analysis should be performed when possible using fresh samples. Samples that must be frozen should be removed and analyzed within a few days. Future studies may desire to try other techniques for freezing ovaries, possibly in water or some other solution. This may reduce the damage to ova and in turn reduce the observed difference in estimated fecundity.

Maturity

At the present time maturity schedules for striped bass are conducted using either the methods of Merriman (1941), Lewis (1962), or Specker et al. (1987), but there has been much debate as to which method is most accurate. The methods used by each researcher were slightly different, as were the criteria used to determined maturity (Table 7). Following is a quick review of the individual studies.

Merriman (1941) examined gonads from 109 female striped bass collected between April and November 1936 and 1937, along Long Island and New England. Fresh gonadal tissue was fixed in either Bouin's solution or 10% formalin. Tissue samples from the 46 Bouin's fixed ovaries were cleared in tolulene, histologically prepared, and stained with Delafield's hematoxylin and eosin. Diameters from 50 oocytes from the anterior, middle, and posterior sections of the ovary were measured under an ocular micrometer. No significant difference between the specific regions was observed, regardless of developmental stage. Sections from the middle of the remaining 63 formalin preserved gonads were macerated until the oocytes floated freely. An ocular micrometer was then used to measure the diameter of 50 oocytes from each ovary under a dissecting microscope. It was concluded that results using Bouin's fixed and formalin fixed ovaries were comparable. Merriman (1941) distinguished two types of ovaries. The first type possessed oocytes which consistently averaged 0.07 mm, but ranged to 0.18 mm.

Table 7. Methods of Merriman (1941), Lewis (1962), and Specker et al. (1987) for determining maturation of female striped bass, which were all used in the present comparative study.

Procedure	Merriman (1941)	Lewis (1962)	Specker et al. (1987)	Present Study (1991)
Fixative	10% Formalin or Bouin's Solution	10% Formalin	Bouin's Solution	Bouin's Solution
Stain	Hematoxylin and Eosin	Hematoxylin and Eosin	Hematoxylin and Eosin	Hematoxylin and Eosin
Method of observation	Ocular micrometer/ Dissecting microscope	Ocular micrometer/ Dissecting microscope	Ocular micrometer/ Dissecting microscope or Camera lucida drawings/digitizing tablet	Microscope slide projector with a digitizing tablet
Number of oocytes measured	up to 50	at least 100	approx. 150	100
Criteria for maturation:				
Minimum oocyte diameter	0.216 mm	0.16 mm	0.15mm	All listed diameters
Other characteristics	Two size classes	Opaquely speckled yolk	Cortical alveoli and/or vitellogenin	All listed characteristics
Minimum number of ova meeting criteria for each schedule	unknown	1 oocyte	1 oocyte	20% of oocytes

These fish were classified as immature. The second type contained oocytes of two definite size categories. Small oocytes, comparable to the first type of ovary, were present as were large oocytes averaging 0.216 mm, but ranging up to 0.58 mm. Those ovaries containing both small and large oocytes were considered mature, with the large oocytes perceived as those that would be released during the following spawning season.

Lewis (1962) sampled gonadal fragments of commercially caught Roanoke River/Albemarle Sound striped bass collected from October 1956 through January 1957, October 1957 through April 1958, and April through September 1960. Fresh gonadal fragments were extracted from the coelom with ear forceps inserted into the vent and preserved in 10% formalin. At least 100 oocytes were randomly selected and measured on a grid-etched slide under a dissecting microscope (45x) with an ocular micrometer. Oocytes were measured on the long axis, since many were asymmetrical. Three general types of oocytes were identified. The type-I oocytes were translucent and ranged in size from 0.03 to 0.23 mm with a mode of about 0.10 mm. Type-II oocytes ranged in size from 0.16 to 0.30 mm and exhibited opaque speckling of the yolk. Those oocytes ranging from 0.33 mm to 1.0 mm and displaying opacity were classified type-III. Type-I oocytes were found year round in all ages and sizes of fish. Type-II were also present year round, but not in all fish. Some of these oocytes were recruited into type-III oocytes during the late spring and early summer. Maturity criteria were as follows: (1) if the largest type-II or type-III oocytes found were equal to or greater than the minimum size of similar oocytes observed for a given month, then the fish was considered mature and expected to spawn during the next spawning season; and (2) fish containing only type-I oocytes were considered immature and were presumed to not be able to spawn for at least one year. Fish containing type-II and type-III oocytes were considered mature.

Specker et al. (1987) collected striped bass from offshore Rhode Island during June and again in October and November of 1985. Fish were also collected from Cat Cove, Massachusetts in August and November of 1985. Fresh tissue samples were removed from the midlength of the ovary and fixed in Bouin's solution. The tissue was dehydrated, cleared in methyl salicylate and blocked in paraffin. Serial sections (10 μm) were stained with hematoxylin and eosin and mounted. Diameters of individual oocytes were determined by either directly measuring oocytes under a dissection microscope using an ocular micrometer or indirectly by measuring camera lucida drawings. Each method produced the same results. Three phases of oocyte development were established by Specker and co-workers (1987). Primary growth oocytes (similar to Lewis' type-I) were found in all fish examined. These had a mode diameter of 0.07 mm and appeared to still be in a gonadotropin-independent stage of development. Samples from June indicated the presence of cortical alveoli (yolk vesicles). These are translucent spheres in the periphery of the ooplasm, which indicate the beginning of the gonadotropin-dependent phase of development, perhaps as early as June. These oocytes ranged in diameter from 0.12 to 0.22 mm. This stage corresponds with Lewis' type-II oocytes. In some ovaries collected during October and November, noticeably larger developing oocytes were present in addition to those previously described. These oocytes ranged from 0.22 to 0.36 mm in diameter and had entered the pituitary-dependent vitellogenic stage. Cortical alveoli appeared to be larger in these oocytes and staining was more intense than other oocytes. These oocytes parallel Lewis' type-III stage of development.

In the present study, all three methods used on females sampled from the Roanoke/ Albemarle system produced similar maturity schedules. This suggests that the three methods can be used interchangeably in determining a maturity schedule. However, there are a number of other factors that must be considered.

These fish were collected on or near the spawning grounds just prior to, or in a few cases, just after spawning. Maturing oocytes will be most developed during this time of the year. Prior to spawning, developing ova change in appearance from small and transparent to large, opaque, and clearly discernible, filled with yolk material; most becoming round and transparent just prior to spawning. Oocytes are at maximum diameter during this period; thus, the number of oocytes reaching minimum diameter criteria will be greatest at this time. Because the overall maturation process requires many months to complete, and oocytes undoubtedly do not develop at the same rate in all fish, the resultant maturity schedule using this percentage criterion will likely be influenced by the season of sampling. Fish collected in this study were sampled during the spring spawning season; thus, any effect of variation in ovarian development throughout the year was not observed.

Of the three studies, only Lewis (1962) may have collected females on or near the spawning grounds during the spawning season. Merriman (1941) sampled female striped bass in ocean waters off Connecticut from April through November; Specker and colleagues (1987) sampled offshore Rhode Island in June, October, and November, and from Cat Cove, Massachusetts in August and November. Maturation schedules determined during other seasons in the year may change with the development of oocytes. This may contribute to a portion of the variation in maturity schedules derived by each researcher.

Another key point which must be addressed, but cannot be defined, is the presence or absence of any level of cutoff in the previous studies. None of the previous studies indicated whether a female would be considered mature if a single oocyte was found to meet their minimum criteria for maturity or conversely, if a rigid percent of mature oocyte criteria was used. Lewis (personal communication, 7/1991) indicated that a single oocyte criterion was used in his (1962) study. Specker and colleagues (1987)

also utilized a maturity criterion of one oocyte exhibiting the appropriate characteristics when determining maturation (J.L. Specker, University of Rhode Island, personal communication, 6/20/1991). Either of these conditions will influence the level of maturity determined for each study. If fish were considered mature when only a few oocytes reached minimum diameter criteria, this may overestimate maturity for those fish; conversely, if a high level was used, it may underestimate the actual number of mature females sampled. In this study, a 20% minimum criteria was used as the level at which females were considered mature. However, results utilizing the 10% or 30% minimum cutoff would have been similar.

The 20% level was deemed reasonable and believed to best represent the population observed. This level may not be appropriate for fish sampled during other seasons, as the variation in gonadal growth may require a reduction of this level. Fish containing less than 20% mature oocytes were believed to be maturing, but may not spawn during the imminent spawning season. Maturing oocytes produce ovarian steroid hormones, which stimulate the release of hypothalamic and pituitary gonadotropins resulting in ovulation and the release of the eggs. It is unknown whether levels of ovarian steroid hormones from fish containing very few maturing oocytes would be sufficient to bring about ovulation and subsequent release of viable eggs. Even though these fish possessed some mature oocytes, they were considered to be maturing, but not yet sexually mature.

In the present study, oocyte diameters were quite variable both among fish and within an individual ovary (0.02 mm to over 1 mm). DeArmon (1948) suggested that ovaries from female striped bass may contain eggs for three spawning seasons. This may explain the variation of oocytes within each fish. To address this issue, ovarian tissue from three spent females was examined. Oocytes were present in the bloody tissue of the spent ovary, with occasional larger oocytes interspersed among the more numerous small oocytes. Results from this small sample size supports DeArmon's (1948) hypothesis in

that the smallest eggs may be retained for spawning in subsequent years, but the retention time for these eggs could not be estimated. The largest oocytes most likely were remnants of the eggs spawned and would be resorbed within several days.

It appears that the age to maturity of female Roanoke striped bass is much earlier than northern populations; one exception was a study by Jones et al. (1977) on female striped bass from the Potomac River which produced results similar to the present study. This early maturation phenomenon has increased since the late 1950s. The percent maturity of age 3 females has changed from less than 5% to about 15% in the early 1980s, to over 40% in the early 1990s (Table 8). The present level of over 40% for age 3 females is a very sharp knife-edge. Future emphasis needs to be placed upon possible maturity of age 2 females. Even though there were no age 2 females observed to be mature in this study, it seems possible that there may be a small percentage which are sexually mature.

Since similar methodologies were used in all Roanoke River maturation studies (e.g., Lewis 1962; Harriss and Burns 1983; Harriss et al. 1984), this early-maturation phenomenon appears to be real and not due to investigator error. The cause of this phenomenon is unclear, but several factors may interact. Factors may cause an increased stress level for a population, either due to poor environmental conditions (Coutant and Benson 1990), intense fishing pressure, and/or genetic differences (Payne 1990) caused by historical stocking practices.

Another factor affecting age to maturity is latitude of the population. Theoretically, fish at lower latitudes should mature quicker due to warmer waters bringing about earlier spawning seasons and a resulting longer growing season (Setzler et al. 1980, ASMFC 1981). A latitudinal component is evident in Table 8.

A significant proportion of age 3 females (44%) in the Roanoke had maturing ovaries; however, it is unclear how much the eggs from these fish contribute to the form-

ing year class. Several researchers familiar with the Roanoke population believe that the young mature females do not produce eggs that are as viable as those from large mature females. Monteleone and Houde (1990) believe that Chesapeake Bay female striped bass under 10 pounds have a lower egg viability rate. Even so, 44% of age 3 female striped bass from the Roanoke River produced eggs which were considered mature and would have been spawned.

Table 8. Maturation schedules of female striped bass from the United States eastern seaboard.

River system	Year	Age 3	4	5	6	7	8	9	Investigator
Offshore Connecticut	1936 & 1937		25	75	95				Merriman (1941)
Offshore Rhode Island & Massachusetts	1984 thru 1988	[a]0 [b]0	8 20	33 37	77 78	100 100	100 100		Specker et al. (1989)
Hudson River	1976	4	7	21	47	87	90	100	McClaren et al. (1981)
	1977	0	5	21	62	90	92	100	" " "
Potomac River	1974 thru 1976	44	79	99	100				Jones et al. (1977)
Roanoke River	1957	4	78	100	100				Lewis (1962)
	1958	4	94	100	100				" "
	1981	18	60	85	92	100			Harriss & Burns (1983)
	1982	17	54	83	100	100			Harriss et al. (1984)
	1989 & 1990	44	93	95	100				Present study

[a] Fish collected during May and June sampling period.
[b] Fish collected during September-November sampling period.

CONCLUSIONS AND RECOMMENDATIONS

1. The three common methodologies for determining maturation rates of female striped bass (Merriman 1941, Lewis 1962, Specker et al. 1987) produce similar maturation schedules when used on fish collected near spawning grounds in the spring.

2. Female striped bass in the Roanoke/Albemarle system mature at an earlier age than those of other systems on the eastern seaboard farther north; about 44% of the age 3 females collected in 1989 and 1990 were sexually mature. The maturation schedule was 93% at age 4, 95% at age 5, and 100% at age 6. Whether these young mature females will produce viable eggs and contribute to the recruiting year class is unknown.

3. The age at which youngest Roanoke females mature appears to be decreasing over time. Females examined in the late 1950s exhibited a maturity of only 4% at age 3, 78-94% at age 4, and 100% mature by age 5. In the early 1980s, about 18% of age 3 females were mature, 54-60% of age 4 females, 83-85% at age 5, and 92-100% by age 6.

4. Fecundity of Roanoke female striped bass is highly predictable on the basis of age, fish length, and body weight. A mature age 3 female produces about 200,000 eggs. The rate of increase is about 200,000 eggs per year until about age 6; fecundity increases exponentially with a maximum estimate of about 5,000,000 for a 16-year old fish.

5. Fresh gonadal tissue, rather than frozen tissue, is preferable for fecundity studies because of an egg fragmentation problem, which increases sample workup time and decreases the accuracy of the estimate.

6. Any one of the three maturation methods will give a similar maturity schedule during the spawning season. Recommendation for further study would include a comparison of the three methods during times other than the spring spawning season to determine variability associated with developing gonads. The preferred sampling time for this study would be from late summer through late fall.

7. Sampling strategies associated with future studies should include more age 2 fish, as well as more small age 3 and age 4 females. This is possible through use of gill nets or purchase of the fish from commercial fishermen.

8. Recomendation for future management practices include the continued harvesting of older, larger fish until the viability of eggs produced from mature three year old females can be determined.

LITERATURE CITED

ASMFC (Atlantic States Marine Fisheries Commission). 1981. Interstate fisheries management plan for the striped bass of the Atlantic Coast from Maine to North Carolina. Fisheries Management Report for Project NA-80-FA-00017, Tidal Fisheries Division, Maryland Department of Natural Resources.

Berlinsky, D.L., and J.L. Specker. 1991. Changes in gonadal hormones during oocyte development in the striped bass, Morone saxatilis. Fish Physiology and Biochemistry 9:51-62.

Cailliet, G.M., M.S. Love, and A.W. Ebeling. 1986. Fishes: A field and laboratory manual on their structure, identification, and natural history. Wadsworth Publishing Company, Belmont, CA.

Chafee, J.H. 1980. The outlook for striped bass recovery, pp. 5-7. in H. Clepper (editor). Proceedings of the Fifth Annual Marine Recreational Fisheries Symposium. Sport Fishing Institute, Washington, DC, USA.

Coutant, C.C., and D.L. Benson. 1990. Summer habitat suitability for striped bass in Chesapeake Bay: reflections on a population decline. Transactions of the American Fisheries Society 119(4):757-778.

DeArmon, I.A., Jr. 1948. Sampling techniques on the ovary of the striped bass, Roccus saxatilis (Walbaum). M.S. Thesis, Virginia Polytechnic Institute., Blacksburg. 40 pp.

Doroshev, S.I. 1970. Biological features of the eggs, larvae and young of the striped bass [Roccus saxatilis (Walbaum)] in connection with the problem of its acclimation in the USSR. Journal of Ichthyology 10:235-248.

Forrester, C.R., A.E. Peden, and R.M. Wilson. 1972. First records of the striped bass, (Morone saxatilis), in British Columbia waters. Journal of Fisheries Board of Canada 29:337-339.

Frie, R.V. 1982. Measurement of fish scales and backcalculation of body lengths using a digitizing pad and microcomputer. Fisheries 7(6):5-8.

Groman, D.B. 1982. Histology of the striped bass. American Fisheries Society Monograph 3. Bethesda, MD, USA.

Hardy, J.D., Jr. 1978. Development of fishes of the Mid-Atlantic Bight: An atlas of juvenile stages. Vol. III. Aphredoderidae through Rachycentridae. Biological Services Program, Fish and Wildlife Service, U.S. Department of the Interior, FWS/OBS-78/12.

Harriss, R.C., Jr., and B.L. Burns. 1983. An investigation of size, age, and sex of North Carolina striped bass. North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries, Morehead City, Annual Progress Report for Project AFC-18-2.

Harriss, R.C., Jr., B.L. Burns, and R.A. Rulifson. 1984. An investigation of size, age, and sex of North Carolina striped bass. North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries, Morehead City, Annual Progress Report for Project AFC-18-3.

Harris, R.C., Jr., B.L. Burns, H.B. Johnson, and R.A. Rulifson. 1985. An investigation of size, age, and sex of North Carolina striped bass. North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries, Morehead City, Completion Report, Project AFC-18.

Hassler, W.W., N.L. Hill, and J.T. Brown. 1981. The status and abundance of striped bass, Morone saxatilis, in the Roanoke River and Albemarle Sound, North Carolina, 1956-1980. Special Scientific Report No. 38, North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries, Morehead, NC. 156 pp.

Holland, B.F., Jr., and G.F. Yelverton. 1973. Distribution and biological studies of anadromous fishes offshore North Carolina. North Carolina Department of Natural and Economic Resources, Division of Commercial and Sports Fisheries, Morehead City, NC, Special Scientific Report Number 24, 132 pp.

Hollis, E.H. 1967. Investigations of striped bass in Maryland. Maryland Department of Chesapeake Bay Affairs, Federal Aid in Fish Restoration F-3-R, Final Report 95 pp.

Jones, P.W., J.S. Wilson, R.P. Morgan, II, H.R. Lunsford, Jr., and J. Lawson. 1977. Potomac River fisheries study; striped bass spawning stock assessment. Interpretive report 1974-1976. University of Maryland, Chesapeake Biological Laboratory, [UMCEES]-CBL 77-56, Solomons, MD, USA.

Kimura, D.K., and J.J. Lyons. 1991. Between-reader bias and variability in the age-determination process. National Oceanic and Atmospheric Administration Fishery Bulletin 89:53-60.

Lewis, R.M. 1962. Sexual maturity as determined from ovum diameters in striped bass from North Carolina. Transactions of the American Fisheries Society 91:279-282.

Lewis, R.M., and R.R. Bonner, Jr. 1966. Fecundity of the striped bass, Roccus saxatilis (Walbaum). Transactions of the American Fisheries Society 95: 328-331.

Manooch, C.S. III, and R.A. Rulifson, editors. 1989. Roanoke River Water Flow Committee Report: A recommended water flow regime for the Roanoke River, North Carolina, to benefit anadromous striped bass and other below-dam resources and users. NOAA Technical Memorandum NMFS-SEFC-216.

Magnin, E., and G. Beaulieu. 1967. Le bar, Roccus saxatilis (Walbaum), du Fleuve Saint-Laurent. Naturaliste Canadien (Quebec) 94:539-555.

Mayer, I., S.E. Shackley, and J.S. Ryland. 1988. Aspects of the reproductive biology of the bass, Dicentrarchus labrax L. I. An histological and histochemical stucy of oocyte development. Journal of Fish Biology 33:609-622.

McLaren, J.B., J.C. Cooper, T.B. Hoff, and V. Lander. 1981. Movements of Hudson River striped bass. Transactions of the American Fisheries Society 110:158-167.

Merriman, D. 1941. Studies of the striped bass (Roccus saxatilis) of the Atlantic Coast. United States Fish and Wildlife Service Fishery Bulletin 50(35):1-77.

Monteleone, D.M., and E.D. Houde. 1990. Maternal effects on growth of larvae, and susceptibility to predation of eggs and larvae of Chesapeake Bay striped bass. University of Maryland, Chesapeake Biological Laboratory, [UMCEES]-CBL 90-010, Solomons, MD, USA.

Nielsen, L.A., and D.L. Johnson. 1983. Fisheries Techniques. American Fisheries Society. Bethesda, MD, USA.

Payne, E.S. 1990. Genetic heterogeneity of Roanoke River striped bass. M.S. Thesis, East Carolina University, Greenville. 75 pp.

Pearson, J.C. 1938. The life history of the striped bass, or rockfish, Roccus saxatilis (Walbaum). United States Bureau of Fisheries Bulletin 49:825-860.

Raney, E.C. 1952. The life history of the striped bass, Roccus saxatilis (Walbaum). Bulletin of the Bingham Oceanographic Collection, Yale University 14(1):5-97.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 191. 382 pp.

Rulifson, R.A., M.T. Huish, and R.W. Thoesen. 1982. Anadromous fish in the southeastern United States and recommendations for development of a management plan. United States Fish and Wildlife Service, Fishery Resources, Region 4, Atlanta, GA. 525 pp.

Rulifson, R.A., D.W. Stanley, and J.E. Cooper. 1988. Striped bass and the food chain: cause for concern? American Water Resources Association, Technical Publication Series TPS-88-1:177-187.

Rulifson, R.A. 1989. Abundance and viability of striped bass eggs spawned in the Roanoke River, North Carolina, in 1988. Albemarle-Pamlico Estuarine Study, Raleigh, NC, Project No. APES 90-03.

Rulifson, R.A., and C.S. Manooch, III, editors. 1990a. Roanoke River Water Flow Committee report for 1988 and 1989. National Oceanic and Atmospheric Administration, Technical Memorandum NMFS-SEFC-256.

Rulifson, R.A., and C.S. Manooch, III. 1990b. Recruitment of juvenile striped bass in the Roanoke River, North Carolina, as related to reservoir discharge. North American Journal of Fisheries Management 10:397-497.

SAS Institute. 1985. SAS Users's Guide: Statistics, Version 5 Edition. SAS Institute, Inc., Cary, NC, USA.

Scofield, E.C. 1931. The striped bass of California (Roccus lineatus). Bulletin of California Fish and Game 29:1-82.

Setzler, E.M., W.R. Boynton, K.V. Wood, H.H. Zion, L. Lubbers, N.K. Mountford, P. Frere, L. Tucker, and J.A. Mihursky. 1980. Synopsis of biological data on striped bass, Morone saxatilis (Walbaum). National Oceanic and Atmospheric Administration, Technical Report, National Marine Fisheries Service Circular 433.

Specker, J.L., D.L. Berlinsky, H.D. Bibb, and J.F. O'Brien. 1987. Oocyte development in striped bass: Factors influencing estimates of age at maturity. American Fisheries Society Symposium 1:162-174.

Specker, J.L., D.L. Berlinsky, S.J. Parker, and J.F. O'Brien. 1989. Reproductive status of female striped bass. Emergency Striped Bass Study, Annual Striped Bass Workshop, Richmond, VA, January 25-26, 1989.

Tesch, F.W. 1971. Age and growth. Pp. 98-126. In W.E. Ricker (editor). Methods for assessment of fish production in freshwaters, 2nd edition. Blackwell Scientific Publications, Oxford, England.

Trent, L., and W.H. Hassler. 1968. Gill net selection, migration, size and age composition, sex ratio, harvest efficiency, and management of striped bass in the Roanoke River, North Carolina. Chesapeake Science 9:217-232.

USDOI and USDOC (United States Department of the Interior and United States Department of Commerce). 1987. Emergency striped bass research study. Report for 1986. Washington, DC. 79 pp.