REPRODUCTIVE BIOLOGY OF SPANISH MACKEREL, *SCOMBEROMORUS MACULATUS*, IN THE LOWER CHESAPEAKE BAY

A Thesis

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Cynthia L. Cooksey

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INTRODUCTION

The Spanish mackerel, *Scomberomorus maculatus* (Mitchill), is a pelagic, migratory, neritic, sub-tropical species occurring in the western Atlantic from Massachusetts south along the Atlantic coast and through the Gulf of Mexico to the Yucatan Peninsula (Collette & Russo 1984; Collette et al. 1978; Powell 1975). Spanish mackerel support important commercial and recreational fisheries throughout much of their range. In summer they are considered common along the Atlantic coast north to the Chesapeake Bay (Bigelow & Schroeder 1953; Musick 1972). They are distributed in the lower waters of the Chesapeake Bay between April and October (Chittenden et al. 1993a). Water temperatures exceed 17^{0}C when they first arrive there, and temperatures are above 20^{0}C when they become abundant (Chittenden et al. 1993a). Peak abundance in the Chesapeake Bay extends from mid June to late August, but some fish are still present through late September-early October (Chittenden et al. 1993a).

Spanish mackerel have historically shown large fluctuations in abundance in the Chesapeake Bay and mid-

Atlantic region (Chittenden et al. 1993b). Though not common before 1850, by 1866 they had become abundant in the Chesapeake Bay and mid-Atlantic and by 1880 the Chesapeake Bay supported the largest fishery for Spanish mackerel in U.S. waters (Earll 1883; Earll 1887). Thereafter, abundance gradually declined in the Chesapeake Bay and the fishery shifted south. Smith (1907) reported that Spanish mackerel were much less abundant in the Chesapeake Bay than 25 years earlier, and after the early 1900's the largest fisheries were located in Florida waters (Klima 1959; Lyles 1969). Landings have generally been low in the Chesapeake Bay and mid-Atlantic region since 1910 except for a brief period in the 1940's (Chittenden et al. 1993b).

Spanish mackerel reappeared in large numbers in the Chesapeake Bay in the mid 1980's, and they have remained abundant through 1994 (Chittenden et al. 1993b). Reasons for their fluctuations in abundance, especially for the recent period of resurgence, are not known (Chittenden et al. 1993b).

Spanish mackerel have been studied extensively. Most research has been in the southern U.S., primarily in Florida waters where age and growth (Klima 1959; Powell 1975; and Fable et al. 1987), food habits (Naughton and Saloman 1981; Saloman and Naughton 1983; and Finucane et al. 1990), larval distribution (McEachran et al. 1980; Collins and Stender

1987; and Collins and Wenner 1988), and reproduction (Klima 1959; Powell 1975; and Finucane and Collins 1986) have all been studied. Except for recent work on occurrence in Chesapeake Bay waters and documentation of fluctuations in abundance there (Chittenden et al. 1993ab), no work has been done on Spanish mackerel north of Cape Hatteras, NC since Earll (1883/1887) and Ryder (1882) more than 100 years ago.

My study addresses the reproductive biology of Spanish mackerel in the lower Chesapeake Bay to help explain how they use this area and to suggest possible reasons for their resurgence in the mid 1980's. I describe microscopic and macroscopic gonad staging criteria, spawning season, spawning location, spawning pattern, sex ratios, length-at-maturity and batch fecundity for this species.

Material and Methods

Data Collection

In 1993 (1,127 fish) and 1994 (1,487 fish) a total of 2,614 fish were purchased from catches of commercial pound nets, gill nets and haul seines in the Chesapeake Bay at Lynnhaven Inlet, Poquoson Flats, York River, Mobjack Bay and Gwynn's Island, and in the Atlantic at Cape Hatteras, NC and Oak Hill, FL (Figure 1). All possible size grades were purchased in either 50 or 25 lb boxes, although total catch was purchased when only smaller quantities were available. Catches were purchased at dockside or from dealers, points at which the catch has been sorted to species and size grade, thus making them the best interception points for data (Chittenden 1989a). Fish were purchased weekly or fortnightly in the period May through October both years. In general, the York River and Mobjack Bay were sampled at least once a week, the other locations more infrequently.

Because Spanish mackerel are available in the Chesapeake Bay only from May through October, additional fish were purchased when possible from Cape Hatteras (in

1993: May 12, 19, September 27 and October 11; in 1994: October 30) and from Florida waters at Oak Hill, north of Cape Canaveral (in 1993: April 12; in 1994: December 12) to evaluate their spawning condition at other times of the year.

General Biological Data

All fish purchased were measured on electronic measuring boards (Limnoterra Atlantic Inc. MFR.) to record fork length (FL) to the nearest mm, total weight (TW) and gonad weight (GW) to the nearest gram, and macroscopically determined sex and gonad stage. Macroscopic gonad stages were based on criteria summarized in Table 1, a system similar to ones in Macer (1974), Barbieri (1993), and Lowerre-Barbieri (1994) which stabilize gonad stage criteria for multiple spawning fishes, thereby reducing confusing terminology. Ovaries were removed and prepared for histologic examination to verify macroscopic gonad stages, assess spawning patterns and determine end of spawning based on the occurrence of atresia (Hunter and Macewicz 1985a; Hunter and Macewicz 1985b).

To prepare for histologic study, a thin cross section was removed from the right ovary, placed in buffered 10%

Table 1. Description of macroscopic and microscopic gonad staging criteria for female Spanish mackerel (*Scomberomorus maculatus*). Macroscopic criteria refer to whole fresh ovaries. Abbreviated gonad stage names and gonad stage numbers in parentheses.

Gonad Stage	Macroscopic Criteria	Microscopic Criteria
Immature (IM, 1)	ovaries very small (<5% of body cavity), light pink in color and translucent, tubular in shape.	only primary growth oocytes present, no excess ovarian tissue present, thin ovarian membrane.
Developing (DE, 2)	ovaries small to medium (5-50% of body cavity), tubular with no or few oocytes visible, brown to light red/orange in color.	primary growth, cortical alveoli and a very few partially yolked oocytes present.
Fully Developed (FD, 3)	ovaries large to very large (50% or more of body cavity up to all available space), firm with yolked oocytes, light red to yellow.	primary growth to fully yolked oocytes, no remnants of hydrated eggs or post-ovulatory follicles (pof's), some atresia may be present.
Gravid (GR, 4)	ovaries large to very large (50%to almost all available space in body cavity), firm with many hydrated ooctes visible, light red to yellow.	primary growth to hydrated oocytes present, some atresia may be present.
Running Ripe (RR, 5)	ovaries large to very large (50% to almost all available space in body cavity), very soft with hydrated oocytes collected in lumen of ovaries, light red to yellow.	primary growth to hydrated oocytes, oocytes have begun ovulation, very fresh pof's present, some atresia may be present.
Partially Spent (PS, 3a)	ovaries large to very large (50% to almost all available space in body cavity), yolked oocytes visible, spawning mark on ventral surface of ovaries near posterior end, red to dark orange.	primary growth to fully yolked oocytes, pof's present or remnant hydrated oocytes, some atresia present.
Spent (SP, 6)	ovaries small to medium (5-50% of body cavity), flaccid and watery, some yolked oocytes, red to dark red.	major atresia occuring throughout ovary of all oocyte stages except primary growth.
Resting (RE, 7)	ovaries very small (<5% body cavity), no oocytes visible, dark red.	only primary growth oocytes present, a large amount of excess ovarian tissue present, thick ovarian membrane

formalin for at least 24 hr, and then placed in 70% ethanol for at least 24 hr. The section was then removed and placed in a tissue cassette in fresh 70% ethanol. Sections were then embedded in paraffin, further sectioned to 5-6 μm thickness and, finally, stained with Harris' Hematoxylin and Eosin Y.

Microscopic gonad staging was based on the occurrence of oocytes in the following cellular stages: primary growth, cortical alveoli, fully yolked oocytes, final maturation (yolk coalescing, when yolk gobules fuse together, and hydration) and atretic (Wallace and Selman 1981). The presence of post-ovulatory follicles (pof's) was used to determine partially spent fish (Alheit et al. 1984; Hunter et al. 1985). The appearance of these microscopic gonad stages is described in the results section "Description of Microscopic Gonad Stages". Percent agreement was calculated between macroscopic and microscopic gonad staging in females to evaluate accuracy of the macroscopic method. I assumed microscopic staging was more accurate, because it describes cellular changes.

Oocyte diameters were measured on two fish to assess whether Spanish mackerel exhibit indeterminate or determinate fecundity. These patterns are distinguished (Hunter et al. 1985) by a continuous size distribution of oocyte diameter (indeterminate) or a discontinuous size distribution (determinate). To do so, oocytes were hydraulically separated from the ovarian tissue and placed in 2% buffered formalin (Lowerre-Barbieri and Barbieri 1993). The mixture was then stirred for 30 sec to minimize settling bias, and then one 5 ml sample was pipetted out and placed in a gridded petri dish. Finally, maximum diameter was measured on 500 oocytes for each fish using the Biosonic Optical Pattern Recognition System.

Spawning Season

Microscopic gonad staging was primarily used to describe the spawning season. This was done by calculating frequencies of the gonad stages. However, the gonadosomatic index (GSI) was also used to determine the general overall spawning season:

$$GSI = (GW/SW) \times 100$$

where:

SW = somatic weight expressed as TW-GW

Somatic weight was used to reduce GSI variance.

Spawning Location

Spawning locations were assessed by the presence of Gravid and Running Ripe females. These stages contain hydrated oocytes, the final stage of oocyte maturation. Because hydration occurs rapidly and is short lived (Fulton 1898), I took these stages to indicate imminent spawning, thus probable spawning locations. This interpretation seems especially appropriate for Running Ripe females which have ovulated the oocytes into the lumen of the ovary, and are ready to release the oocytes or have already begun to do so.

Finally, I report ten Spanish mackerel, 79-184 mm FL, collected by the VIMS Juvenile Trawl Survey and Beach Seine Survey to help document the use of the Chesapeake Bay area as a nursery. Though I interpret them to indicate survival of Spanish mackerel eggs and larvae spawned in the Chesapeake Bay area, these fish could have been spawned in more southern waters. For a description of the VIMS trawl survey see Chittenden et al. (1989b) and Geer et al. (1990).

Sex Ratios

Chi square analysis (Glenberg 1988) was used to assess significant deviations from a one to one sex ratio for the overall data. Deviations from a one to one sex ratio among size grades, locations, and 100 mm length intervals were also analyzed.

Length-at-maturity

Length-at-maturity was estimated using 645 females (190-360 mm FL) and 836 males (190-360 mm FL) assigned to 10 mm fork length intervals. Fish were considered mature if they were classified into gonad stages 2-7 (Table 1). Percent mature was plotted against mean length by intervals, and mean length at first maturity (L_{50}) was visually estimated as the predicted length at which 50% of the fish are mature.

Batch Fecundity

Batch fecundity was determined gravimetrically on 13 females using the hydrated oocyte method, because the hydrated oocyte is the only distinct stage in multiple spawners (Fulton 1898; Hunter et al. 1985). This method employs the ratio estimate:

$$Y = (y/x)\ X$$

where:

Y = fecundity

y = number of hydrated oocytes in the tissue sample
x = weight of tissue sample
X = weight of ovaries

I used only fully hydrated fish for these counts. Relative batch fecundity, eggs/g , was calculated using ovary-free weight to reduce error in that estimate (Hunter and Goldberg 1980).

Oocyte counts were made on fresh ovaries in 1993 and in June 1994, but fish were preserved in 10% buffered formalin thereafter. Batch fecundities were based on oocyte counts in 16 sections per fish for the first ten fish and eight sections for the last three fish. The 0.2 g tissue sections on which counts were made were gently cut from the ovaries so that hydrated oocytes would not be squeezed out, thus underestimating batch fecundity.

Tissue sections for counting were taken from four areas in each of the first ten fish: the middle of the right ovary, and the anterior, middle and posterior of the left ovary. Four sections were then removed from each area. A randomized complete block ANOVA was used to test for positional effects within ovaries and between pairs of ovaries. In doing so, each ovary was considered a block with four treatments (areas) and four replicates (individual counts) in each treatment. When the ANOVA detected a significant difference between areas, Scheffe's test was used to determine which areas were different. Based on the results of these tests, only two counts were made in each of the four areas for the last three fish.

Simple linear regression was used to describe regressions of batch fecundity on fork length and on somatic weight, and one-way ANOVA was used to test if larger fish have greater relative fecundity and produce more eggs per gram SW (Lowerre-Barbieri 1994).

Results

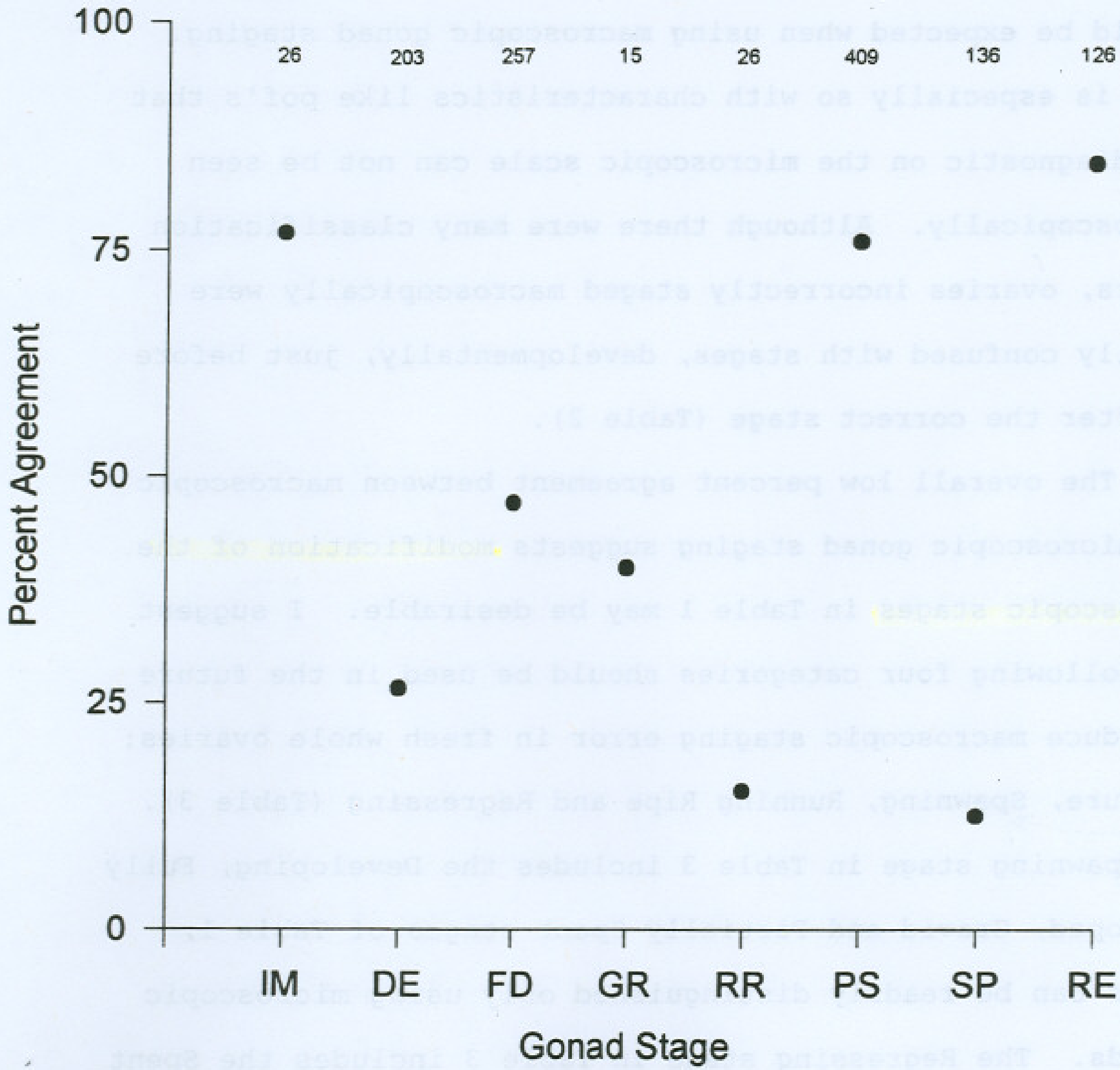
Description of Microscopic Gonad Stages

Spanish mackerel are multiple spawners that exhibit a complex spawning pattern in which females progress through eight distinct microscopic gonad stages. Each stage (Table 1) has a unique microscopic appearance when thin sectioned and stained. The Immature stage is characterized by the presence of only primary growth oocytes and a thin ovarian membrane (Figure 2). This stage occurs only in fish that have never spawned. The Developing stage is characterized by the presence of primary growth, cortical alveoli and a very few, if any, partially yolked oocytes (Figure 3). The Fully Developed stage is characterized by the presence of primary growth to fully yolked oocytes, but no pof's (Figure 4). The Gravid stage is characterized by primary growth to hydrated oocytes (Figure 5). The hydrated oocytes are still inside the follicles of the ovary in this stage. The Gravid stage ovary may also show a few degenerating pof's from an earlier spawning (Figure 5). The Running Ripe stage is characterized by primary growth to hydrated oocytes. Some to most of the hydrated oocytes have been ovulated into the lumen of the ovary (Figure 6). This stage is usually difficult to determine microscopically, because ovulated oocytes may be washed out of the lumen during fixation. If this occurs the ovary may be misidentified as Partially Spent with a few remnant hydrated oocytes. The Partially Spent stage is characterized by primary growth to fully yolked oocytes and the presence of pof's (Figure 7). The Fully Developed thru Partially Spent stages all exhibit some atresia, but not major amounts. The Spent stage is characterized by major atresia throughout the ovary (Figure 8). The Resting stage, finally, is characterized by the presence of only primary growth oocytes and a thick ovarian membrane (Figure 9). It is best distinguished from the Immature stage by the much thicker ovarian membrane.

Agreement Between Macroscopic and Microscopic Gonad Staging Methods

Overall, there was a 53.3% agreement between macroscopic and microscopic gonad staging methods for Spanish mackerel. Agreement was highest, 76.0-84.6%, in the Immature, Partially Spent and Resting stages (Figure 10).

Figure 10. Percent agreement between macroscopic and microscopic gonad stages in female Spanish mackerel by gonad stage. See Table 1 for full gonad stage names. Numbers at top of figure represent numbers staged.



Percent Agreement
100
75
50
25
0
26
203
257
15
26
409
136
126
IM
DE
FD
GR
RR
PS
SP
RE
Gonad Stage

Agreement was intermediate, 26.6-47.1%, in the Developing, Fully Developed and Gravid stages. Agreement was lowest, 12.5-15.3%, in the Running Ripe and Spent stages. Percent agreement is so low in the all of the above stages, because these stages are short-lived and/or occur on a continuum. As a result, large numbers of misclassification errors should be expected when using macroscopic gonad staging. This is especially so with characteristics like pof's that are diagnostic on the microscopic scale can not be seen macroscopically. Although there were many classification errors, ovaries incorrectly staged macroscopically were usually confused with stages, developmentally, just before or after the correct stage (Table 2).

The overall low percent agreement between macroscopic and microscopic gonad staging suggests modification of the macroscopic stages in Table 1 may be desirable. I suggest the following four categories should be used in the future to reduce macroscopic staging error in fresh whole ovaries: Immature, Spawning, Running Ripe and Regressing (Table 3). The Spawning stage in Table 3 includes the Developing, Fully Developed, Gravid and Partially Spent stages of Table 1, stages can be readily distinguished only using microscopic methods. The Regressing stage in Table 3 includes the Spent and Resting stages of Table 1, stages which can only be readily distinguished using microscopic methods.

Table 2. Summary of microscopic gonad stages assigned to macroscopically staged Spanish mackerel ovaries, 1993 and 1994. Data expressed as number of ovaries. See Table 1 for full gonad stage names. Microscopic gonad stages were assumed correct.

Microscopic Stage	Macroscopic Stage IM	DE	FD	GR	RR	PS	SP	RE
IM	20	113	--	--	--	--	--	10
DE	--	54	19	--	--	3	4	5
FD	--	1	121	--	--	90	--	--
GR	--	--	--	6	--	3	--	--
RR	--	--	--	1	4	--	--	--
PS	--	5	109	8	19	311	70	--
SP	--	2	4	--	2	27	17	3
RE	6	26	--	--	--	1	43	105

Table 3. Suggested macroscopic gonad stages and criteria for future use with female Spanish mackerel. These stages are revised from those in Table 1. See text.

Revised Gonad Stage	Macroscopic Criteria
Immature	ovaries very small (<5% of body cavity), light pink in color and translucent, tubular in shape. Includes Immature stage from Table 1.
Spawning	includes Developing, Fully Developed, Gravid and Partially Spent stages from Table 1.
Running Ripe	ovaries large to very large (50% to almost all available space in body cavity), very soft with hydrated oocytes in lumen of ovaries, light red to yellow, includes Running Ripe stage from Table 1.
Regressing	includes Spent and Resting stages from Table 1.

Spawning Season

Spanish mackerel spawn in the Chesapeake Bay area from June through August. No fish are capable of spawning when they begin to appear in May, because they are all in the Immature, Resting and, primarily, Developing stages (Figure 11). Fish are spawning by June because many fish are in the Fully Developed, Gravid, Running Ripe and Partially Spent gonad stages then. Fish with Gravid and Running Ripe ovaries occur only in June, July and August. Developing, Spent and Resting stage ovaries were found throughout the period June through August. Females do not spawn after August, because all females were in either Spent or Resting stages in September, October and December. All advanced oocytes are either atretic or have already been absorbed after August.

Gonadosomatic indices also indicate Spanish mackerel spawn from June to August, with peak spawning in June. Mean GSI's increased greatly from May to June and were generally highest in June (Figure 12). Mean GSI's were high in July and August, though they gradually declined through August, and greatly decreased in September. Mean and, usually, maximum GSI's were low in April, May, September, October and December.

Figure 11. Frequency of microscopic gonad stages for female Spanish mackerel in the Chesapeake Bay by month, 1993-1994. Numbers at top of figure represent numbers staged.

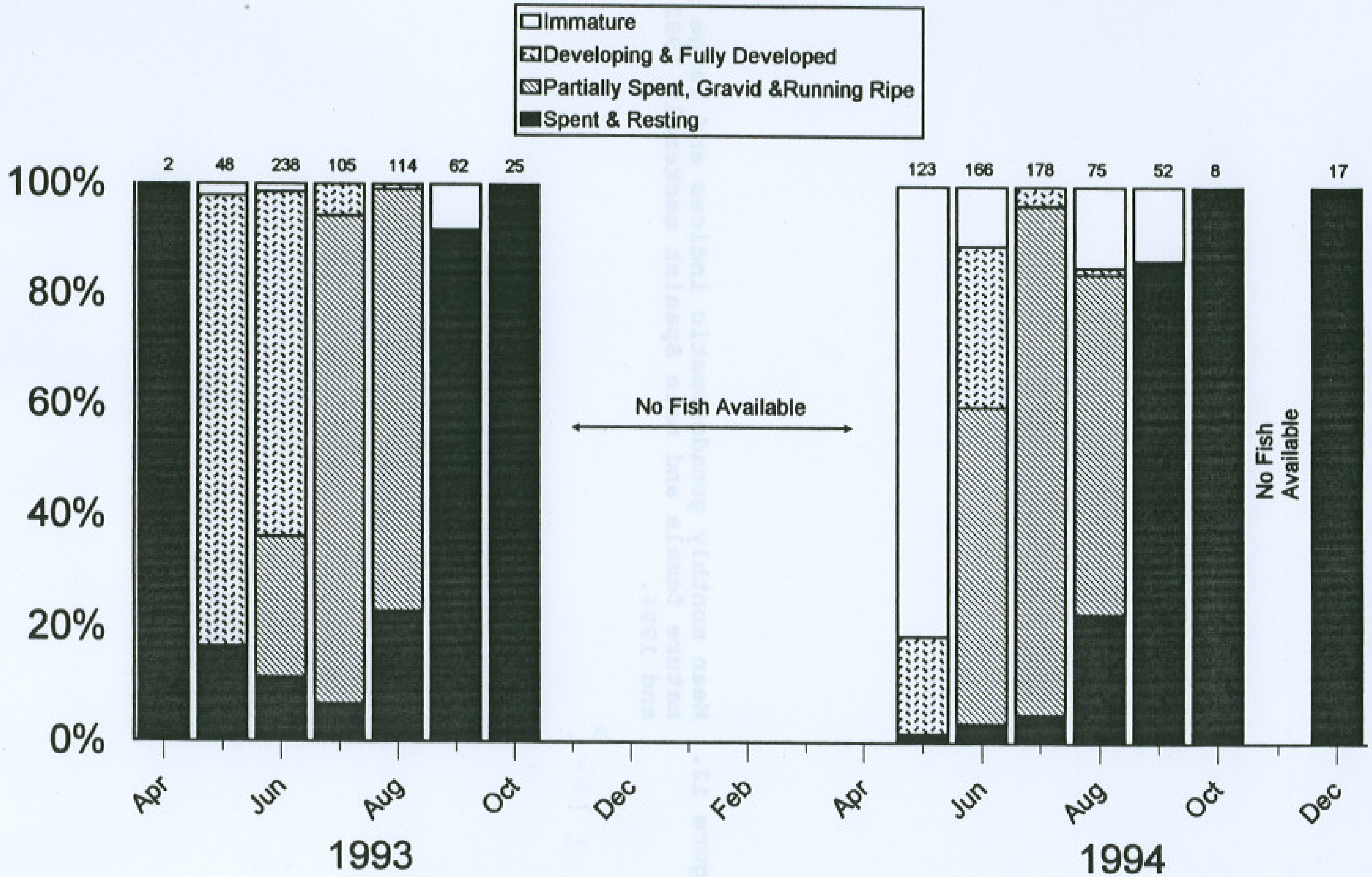
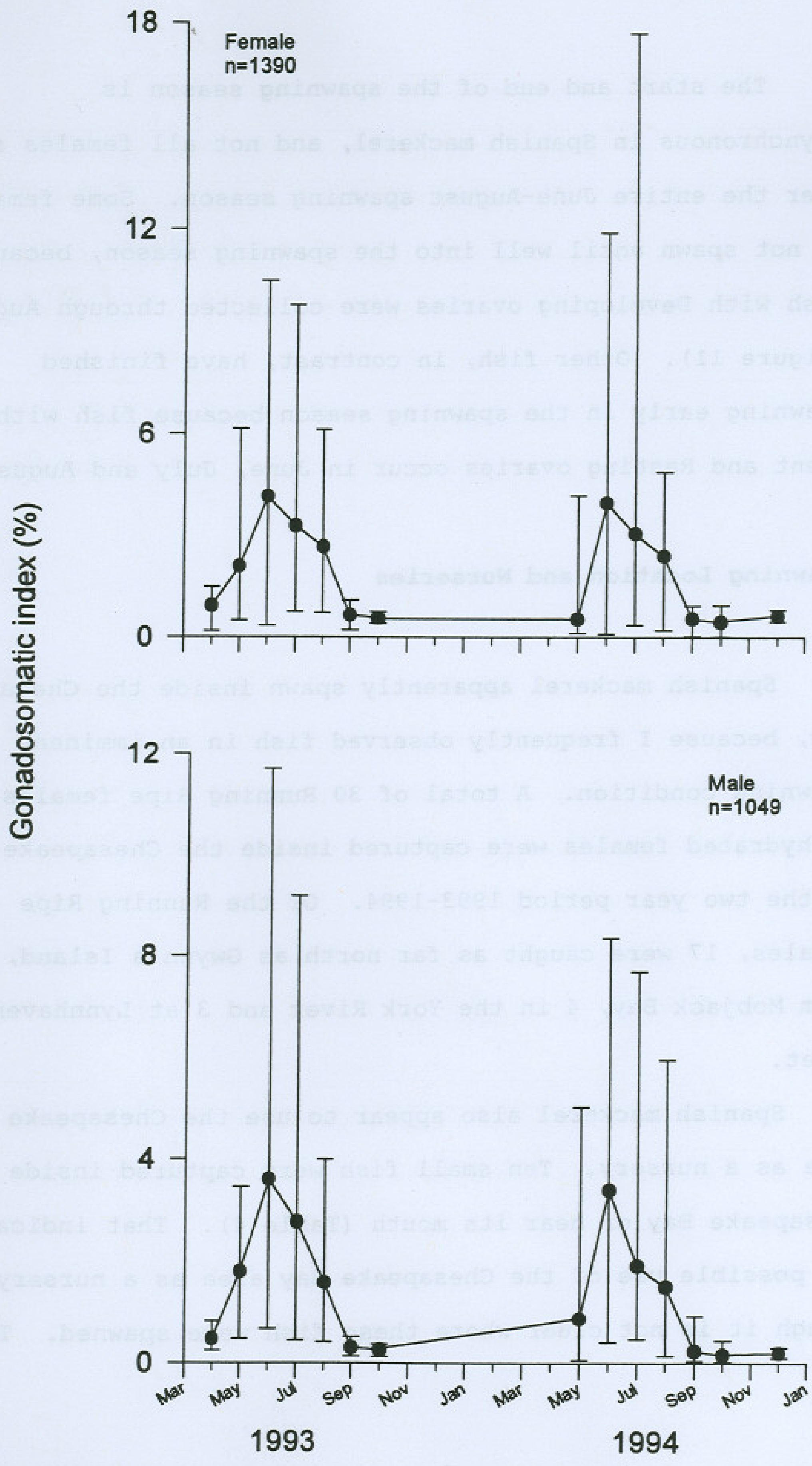

Immature
Developing & Fully Developed
Partially Spent, Gravid &Running Ripe
Spent & Resting
100%
80%
60%
40%
20%
0%
2
48
238
105
114
62
25
123
166
178
75
52
8
17
No Fish Available
No Fish Available
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Aug
Oct
Dec
1993
1994

Figure 12. Mean monthly gonadosomatic indices and range for mature female and male Spanish mackerel, 1993 and 1994.

± 1SD?


Female
n=1390
Male
n=1049
Gonadosomatic index (%)
18
12
6
0
12
8
4
0
Mar
May
Jul
Sep
Nov
Jan
Mar
May
Jul
Sep
Nov
Jan
1993
1994

The start and end of the spawning season is asynchronous in Spanish mackerel, and not all females spawn over the entire June-August spawning season. Some females do not spawn until well into the spawning season, because fish with Developing ovaries were collected through August (Figure 11). Other fish, in contrast, have finished spawning early in the spawning season because fish with Spent and Resting ovaries occur in June, July and August.

Spawning Location and Nurseries

Spanish mackerel apparently spawn inside the Chesapeake Bay, because I frequently observed fish in an imminent spawning condition. A total of 30 Running Ripe females and 25 hydrated females were captured inside the Chesapeake Bay in the two year period 1993-1994. Of the Running Ripe females, 17 were caught as far north as Gwynn's Island, 6 from Mobjack Bay, 4 in the York River and 3 at Lynnhaven Inlet.

Spanish mackerel also appear to use the Chesapeake Bay area as a nursery. Ten small fish were captured inside the Chesapeake Bay or near its mouth (Table 4). That indicates the possible use of the Chesapeake Bay area as a nursery, though it is not clear where these fish were spawned. They

Table 4. Date and location of small Spanish mackerel caught in the Chesapeake Bay area by the VIMS trawl or beach seine survey.

Year	Date	Location	FL (mm)	TL (mm)	TW (g)
1993	0819	Rappahannock River	91	103	5.9
	0902	"	115	127	12.6
	0902	"	96	110	8.0
	0902	"	84	95	5.0
	0902	"	83	94	5.0
	0902	"	79	89	4.0
	0902	"	76	85	3.7
	0908	York River	184	218	66.8
	0913	Rappahannock River	127	146	18.8
	0914	Lower Bay	159	182	39.7
1994	0812	Sandbridge, Va	28		
	0815	Oyster, Va	30		

may or may not represent survival of eggs and larvae spawned in the Chesapeake Bay area.

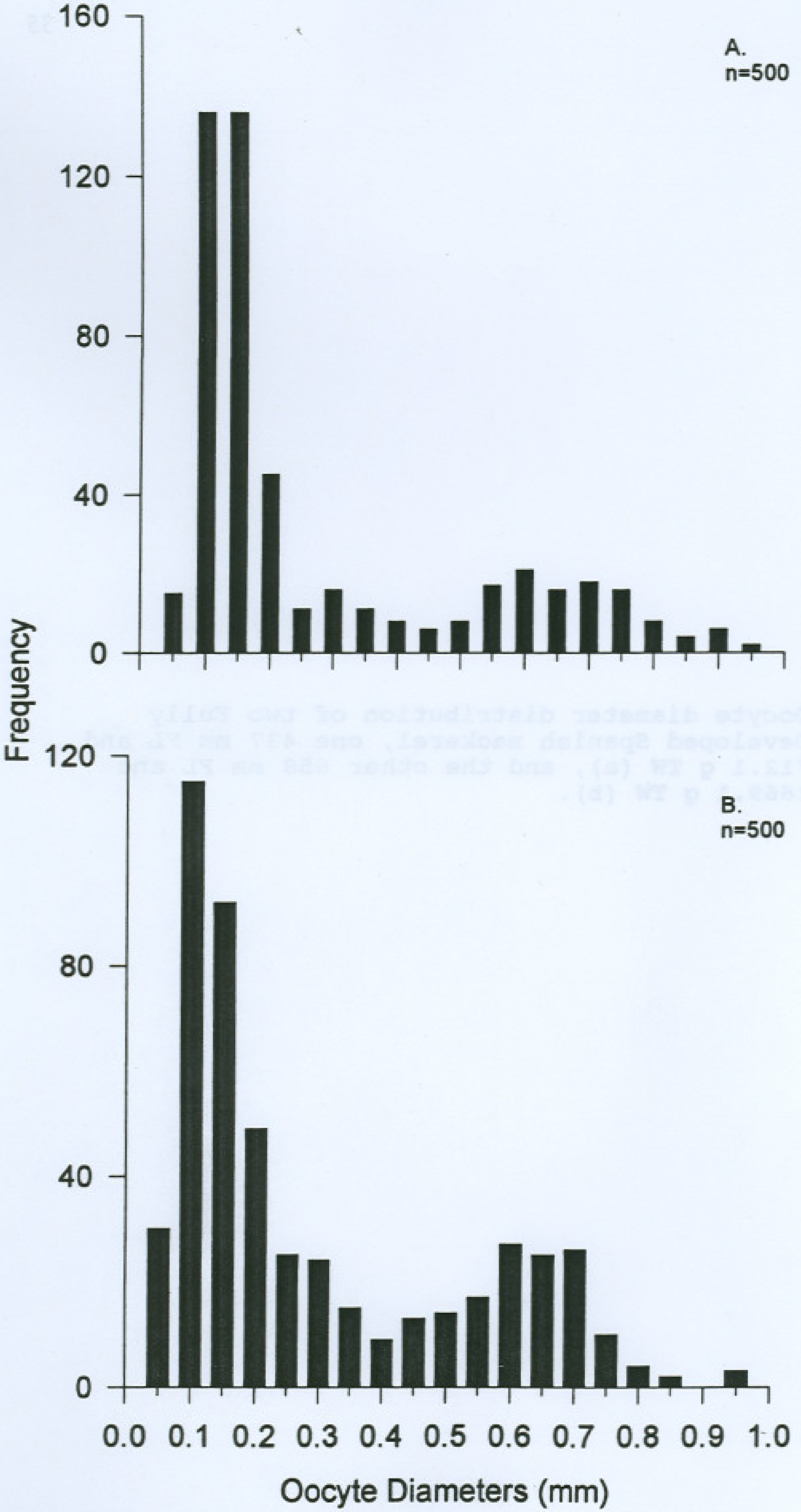
Spawning Pattern

Spanish mackerel are indeterminate spawners, releasing more than one batch of eggs during the spawning season and continuing to mature new batches throughout the season. Oocyte sizes show a continuous distribution characteristic of indeterminate spawners (Figure 13). There are no obvious gaps in the size distribution that would indicate a species with determinate fecundity.

Spanish mackerel are multiple spawners. The Partially Spent stage is generally the most common gonad stage in females during the June-August spawning season (Figure 11). In this stage they have fully yolked oocytes commonly intermixed with pof's, as well as oocytes in the final stage of maturation (yolk coalescing) intermixed with fresh pof's (Figure 14). These phenomena indicate a rapid turnover of oocytes in the ovary, and that new batches of oocytes rapidly mature after a previous spawning.

Spanish mackerel have a complex spawning pattern of eight distinct stages. They exhibit a primary ovarian cycle that is typical of all total and multiple spawners (Figure

Figure 13. Oocyte diameter distribution of two Fully Developed Spanish mackerel, one 437 mm FL and 712.1 g TW (a), and the other 658 mm FL and 2669.1 g TW (b).


160
120
80
40
0
A.
n=500
Frequency
120
80
40
0
B.
n=500
0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
Oocyte Diameters (mm)

15). This primary cycle is characterized by seven stages: Immature, Developing, Fully Developed, Gravid, Running Ripe, Spent, and Resting. Nested within the primary cycle is a secondary cycle that only multiple spawners exhibit. This secondary cycle in characterized by the Partially Spent gonad stage in which multiple batches of oocytes rapidly mature in a single spawning season.

Sex Ratios (all fish - immat. + mat.) Not gear specific

Spanish mackerel sex ratios vary greatly. Overall, males accounted for 44% of the catch and females 56%. This ratio differed significantly from 1:1 (χ^2=40.8, 2 df). Males made up 40% of the catch in 1993 and females 60%, ratios significantly different from 1:1 (χ^2=48, 2 df). Males accounted for 47% of the catch in 1994 and females 53%, ratios not significantly different from 1:1 (χ^2=5.8, 2 df).

Spanish mackerel sex ratios show no trend by month (Table 5). In eight of the fourteen months sampled the ratio differed significantly from 1:1. Of these eight months, there are significantly more females in six months and significantly more males in two.

Sex ratios show no obvious trends between locations

Figure 15. The ovarian cycle of Spanish mackerel. Dark arrows indicate the primary cycle both total and multiple spawners exhibit, open arrows indicate the secondary cycle only multiple spawners exhibit.

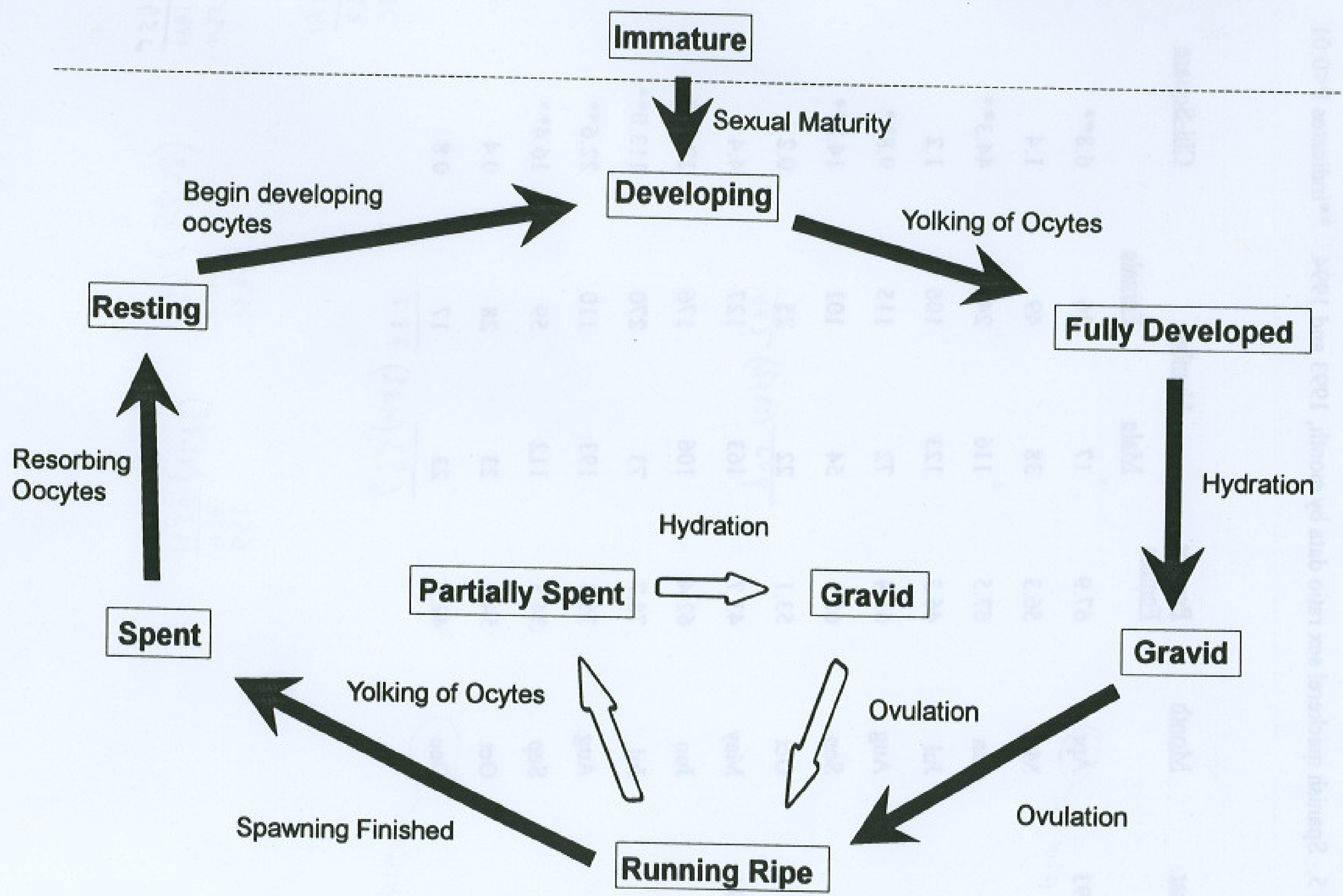

Immature
Sexual Maturity
Developing
Begin developing oocytes
Yolking of Ocytes
Resting
Fully Developed
Resorbing Oocytes
Hydration
Hydration
Partially Spent
Gravid
Spent
Gravid
Yolking of Ocytes
Ovulation
Ovulation
Spawning Finished
Running Ripe

Table 5. Spanish mackerel sex ratio data by month, 1993 and 1994. **indicates P<0.01.

Year	Month	Percent Female	Number Male	Number Female	Chi-Square
1993	Apr	67.9	17	36	6.8**
	May	56.3	38	49	1.4
	Jun	67.5	116	242	44.3**
	Jul	46.2	123	106	1.2
	Aug	61.4	72	115	9.8**
	Sep	65.1	54	101	14.2**
	Oct	53.1	22	25	0.2
1994	May	43.7	163	127	4.4
	Jun	62.4	106	176	17.3**
	Jul	78.7	73	270	113.0**
	Aug.	36.3	193	110	22.6**
	Sep	34.5	112	59	16.4**
	Oct	54.9	23	28	0.4
	Dec	42.5	23	17	0.8

(Table 6). The York River had significantly more females in 1993, but significantly more males in 1994. Some locations have more males while others have more females within years.

Females generally dominated catches of the larger grades and sizes. Grades large and jumbo (1993) and grades medium and large (1994) had significantly more females (Table 7). However, there was no difference between the sexes in the small size grade either year. There were significantly more females in the ranges 400-499 mm and 500-599 mm FL in 1993 and 1994 (Table 8). There were no males above 600 mm in 1993 and none above 500 mm in 1994.

Length-at-Maturity

Spanish mackerel can spawn at small sizes. Size at first maturity (L_{50}) was visually on the plot estimated at 230 mm FL in females and 232 mm in males (Figure 16). All females were mature at 330 mm and all males at 340 mm. There were no females less than 300 mm FL that showed definite signs of spawning, like pof's or hydrated oocytes.

Batch Fecundity

Counts of hydrated oocytes showed positional effects in

Table 6. Spanish mackerel sex ratio data by location, 1993 and 1994. **indicates P<0.01.

Year	Location	Percent Female	Number Male	Number Female	Chi-Square
1993	York River	64.3	218	393	50.1**
	Mobjack Bay	38.2	134	83	12.0**
	Lynnhaven	78.9	16	60	25.4**
	North Carolina	62.5	69	115	11.4**
1994	York River	43.8	263	205	7.0**
	Mobjack Bay	39.2	173	112	13.0**
	Lynnhaven	58.0	181	250	11.0**
	Gwynn's Island	82.6	38	181	93.2**
	North Carolina	55.8	15	19	0.4

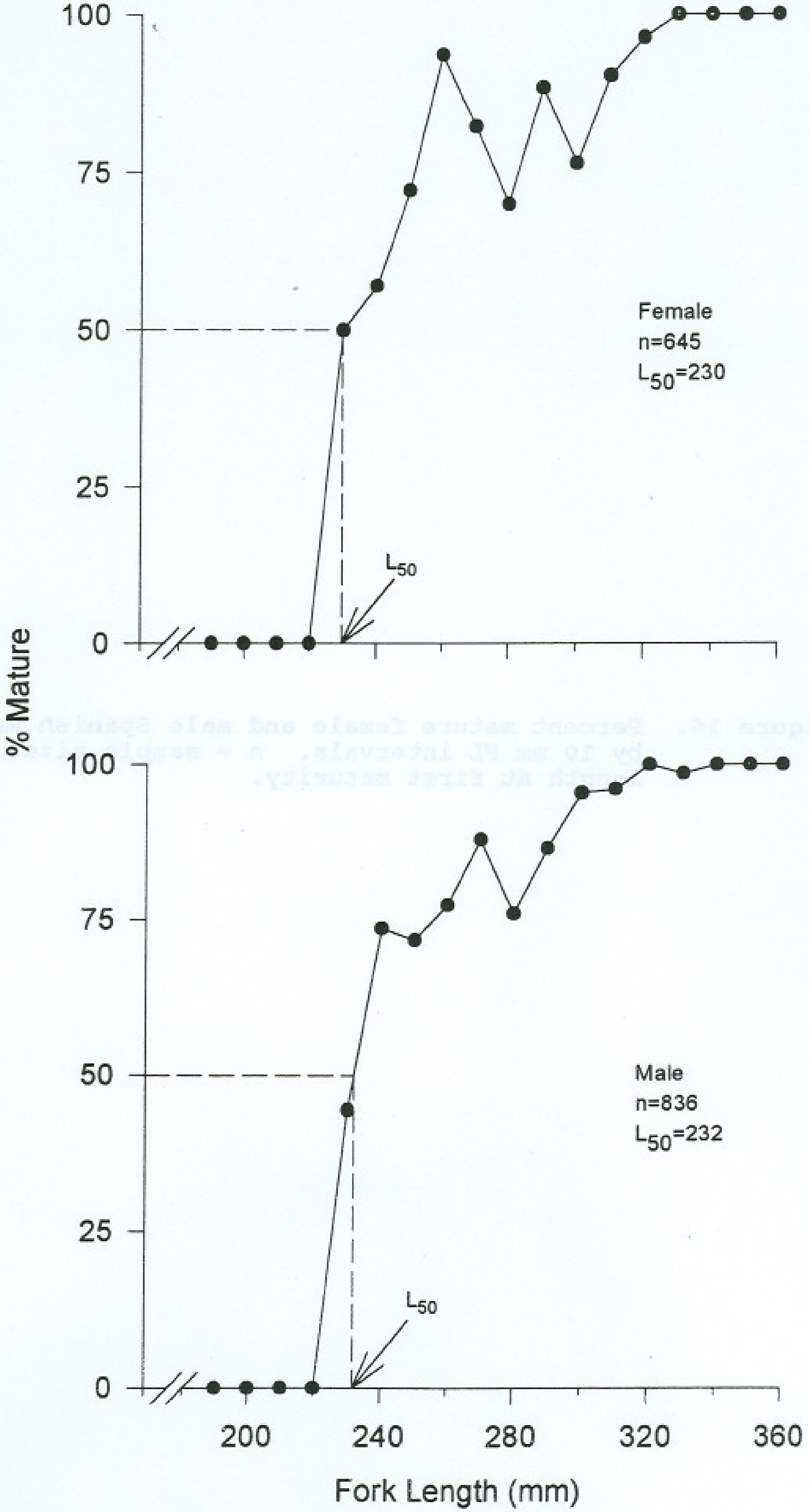
Table 7. Spanish mackerel sex ratio data by commercial size grade, 1993 and 1994. ** indicates P<0.01.

Year	Grade	Percent Female	Number		Chi-Square
			Male	Female	
1993	small	45.0	39	32	0.6
	medium	53.6	77	89	0.8
	large	82.1	18	83	41.8**
	jumbo	100	0	8	8.0**
1994	small	48.3	198	185	0.4
	medium	79.5	28	109	47.8**
	large	87.5	22	154	99.0**

Table 8. Spanish mackerel sex ratio data by size interval, 1993 and 1994. ** indicates P<0.01.

Year	FL Interval (mm)	Percent Female	Number		Chi-Square
			Male	Female	
1993	100-199	33.3	2	1	1.0
	200-299	45.6	56	47	0.6
	300-399	46.0	314	268	3.6
	400-499	82.5	65	308	158.2**
	500-599	90.7	5	49	35.8**
	600-699	100	0	1	1.0
1994	200-299	38.1	256	158	19.0**
	300-399	51.0	405	423	0.2
	400-499	82.1	42	193	97.0**
	500-599	100	0	8	8.0**
	600-699	100	0	1	1.0

Figure 16. Percent mature female and male Spanish mackerel by 10 mm FL intervals. n = sample size. L_{50} = length at first maturity.


Female
n=645
L50=230
L50
Male
n=836
L50=232
L50
% Mature
100
75
50
25
0
200
240
280
320
360
Fork Length (mm)

the ovaries. A randomized complete block ANOVA found significant differences between locations (n=160, F=4.56, P=0.0044)(Table 9). Scheffe's test showed no difference within the left ovary nor between the left and right middle (α=0.05, df=147). The significant difference was between the right middle and the left anterior. As a result, to save counting time, my batch fecundity estimates were based on 2 counts per area after July 6, 1994.

Spanish mackerel batch fecundity ranged from 34,000 to 145,000 eggs per batch. Mean batch fecundity was 74,077 eggs per batch, standard error was 8,571, and the 95% confidence interval was 18,676 (Table 10). Batch fecundity was significantly related to both fork length and somatic weight. Batch fecundity increased significantly with fork length (ANOVA n=13, F=16.34, P<0.001), their regression being (Figure 17):

$$BF = -159{,}197.73 + 610.17\ FL \quad ; \quad (R^2=0.59).$$

Batch fecundity increased significantly with somatic weight (ANOVA n=13, F=4.77, P<0.0004), their regression being (Figure 18):

$$BF = -8{,}210.81 + 160.33\ SW \quad ; \quad (R^2=0.69).$$

Table 9. Results of Randomized Complete Block Analysis of Variance to determine the existence of positional effects in Spanish mackerel ovaries.

n=10

Randomized Complete Block ANOVA

Source	DF	Sum of Squares	Mean Square	F
Model	12	364353.500	303529.458	160.89
Block (fish)	9	3616572.775	401841.419	213.00
Positional Effect	3	25780.75	8593.575	4.56
Error	147	277330.275	1886.601	--
Corrected Total	159	3919683.775	--	--

Table 10. Batch fecundity and sizes of Spanish mackerel, 1993 and 1994.

Year	Collection Date	Eggs/Batch	FL (mm)	TW (g)	SW (g)	GW (g)
1993	0729	88,000	429	758.3	729.2	29.1
	0802	52,000	371	446.4	422.0	24.4
1994	0613	72,000	417	726.2	649.0	77.2
	0620	52,000	336	408.7	371.8	36.9
	0620	63,000	352	469.7	434.8	34.9
	0620	85,000	371	517.7	480.7	37.0
	0620	145,000	439	944.0	844.8	99.2
	0701	44,000	352	396.0	378.9	17.1
	0701	110,000	428	683.9	635.3	48.6
	0706	34,000	335	359.5	335.9	23.6
	0706	96,000	418	601.9	570.4	31.5
	0711	75,000	338	368.7	342.3	26.4
	0810	47,000	384	496.6	476.9	19.7
	mean	74,077	382	552	513	39
	standard error	8,571	11	50	44	7

Figure 17. Regression of batch fecundity on fork length of Spanish mackerel, 1993 and 1994.

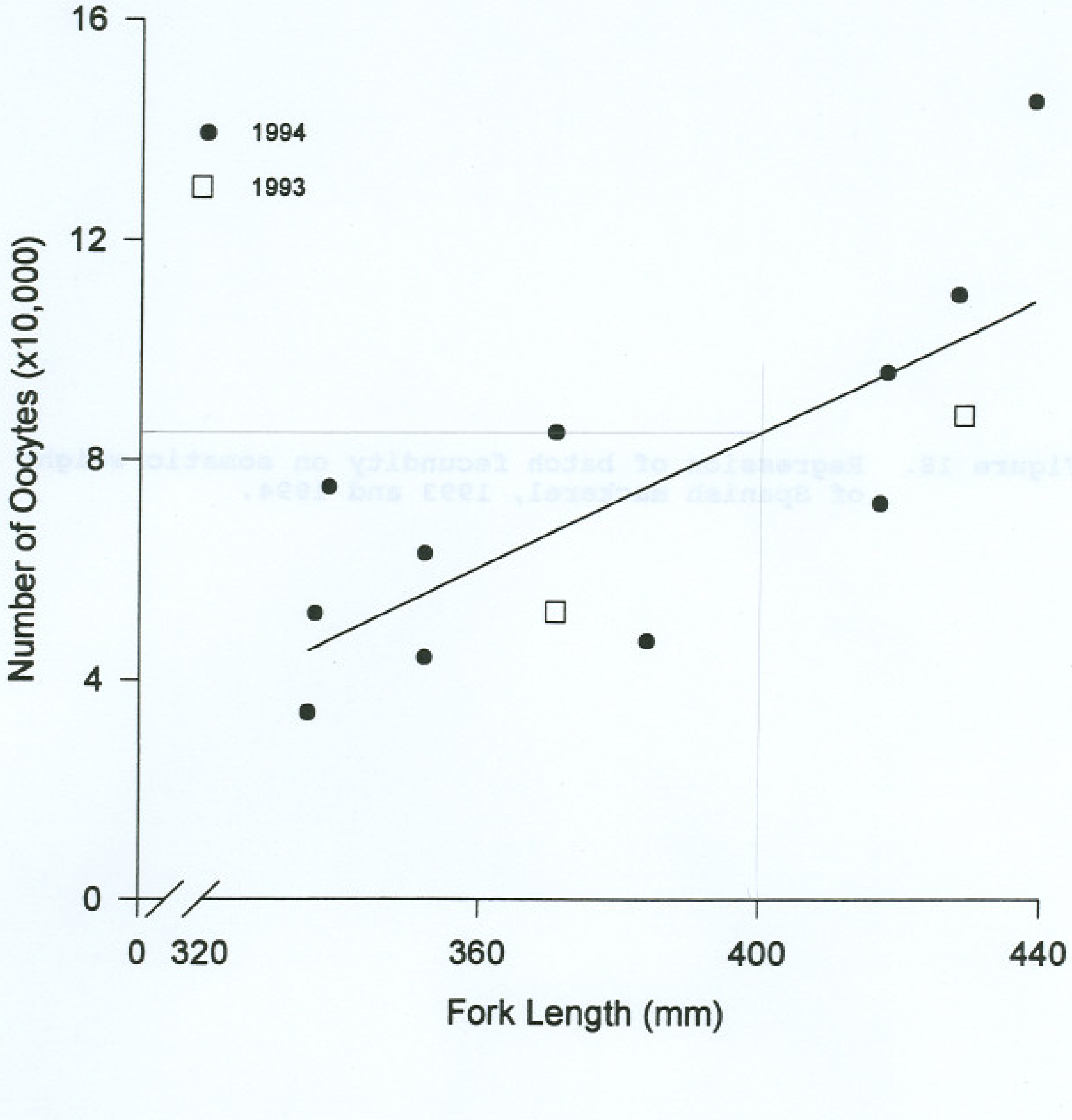
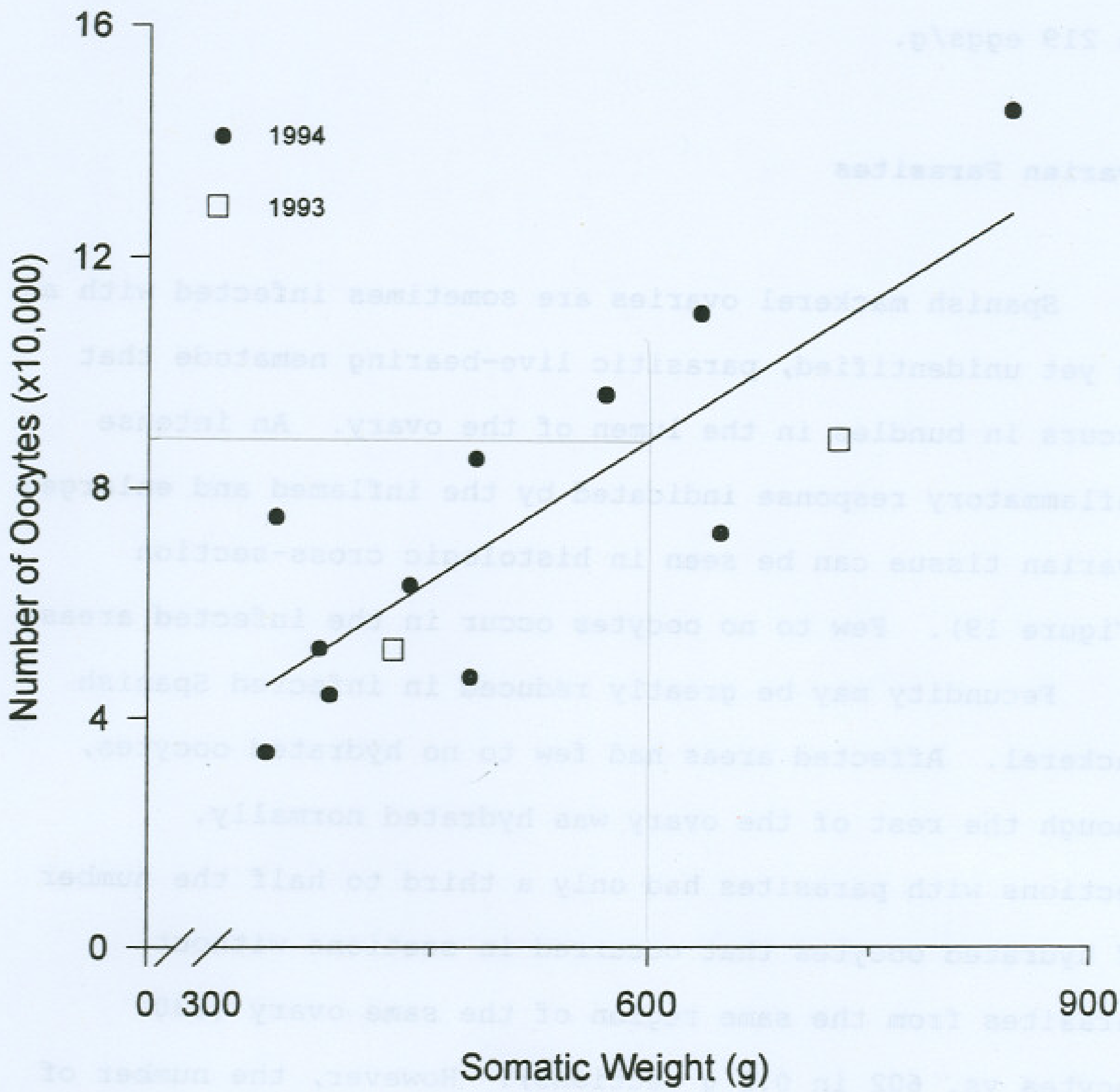

1994
1993
Number of Oocytes (x10,000)
16
12
8
4
0
0
320
360
400
440
Fork Length (mm)

Figure 18. Regression of batch fecundity on somatic weight of Spanish mackerel, 1993 and 1994.



1994
1993
Number of Oocytes (x10,000)
16
12
8
4
0
0
300
600
900
Somatic Weight (g)

Spanish mackerel relative fecundity did not increase with size. Relative fecundity showed no relation to somatic weight (ANOVA n=13, F=0.08, P=0.77), nor with fork length (ANOVA n=13, F=0.04, P=0.84). Spanish mackerel produced on average 143 eggs/g female (±10 SE) and ranged from 98 eggs/g to 219 eggs/g.

Ovarian Parasites

Spanish mackerel ovaries are sometimes infected with an as yet unidentified, parasitic live-bearing nematode that occurs in bundles in the lumen of the ovary. An intense inflammatory response indicated by the inflamed and enlarged ovarian tissue can be seen in histologic cross-section (Figure 19). Few to no oocytes occur in the infected areas.

Fecundity may be greatly reduced in infected Spanish mackerel. Affected areas had few to no hydrated oocytes, though the rest of the ovary was hydrated normally. Sections with parasites had only a third to half the number of hydrated oocytes that occurred in sections without parasites from the same region of the same ovary (230 oocytes vs. 602 in 0.2 g sections). However, the number of parasites in an infected ovary varies greatly from fish to fish. Nematodes were present in two of the thirteen ovaries used to estimate batch fecundity.

Discussion

Spawning Pattern and Gonad Staging

I found that Spanish mackerel are multiple spawners. As such, they have a complex reproductive cycle that includes, in females, eight different microscopic gonad stages distributed into two distinct cycles: a primary cycle that both total and multiple spawners exhibit and a secondary cycle that only multiple spawners exhibit. Though the terminology has changed over the years, previous descriptions of Spanish mackerel reproduction (Kilma 1959; Powell 1975; Finucane and Collins 1986) basically recognize that the species has indeterminate fecundity. However, they have not described the Partially Spent stage that is characteristic of multiple spawners.

I found that Spanish mackerel are indeterminate spawners with asynchronous oocyte development. As such, they continuously mature new batches of eggs to be released throughout the spawning season, though I was not able to determine their spawning frequency. These findings generally agree with earlier studies. Earll (1883) found small oocytes still in the ovary when the first batch of mature oocytes was being spawned and concluded that oocytes were released over an extended period. Powell (1975) also concluded that Spanish mackerel spawn repeatedly over a prolonged spawning season, basing this on their asynchronous development of oocytes, and the occurrence of small larvae throughout the sampling period combined with a pronounced overlap of length ranges. Though they did not present much detail, Finucane and Collins (1986) also reported a prolonged spawning season.

The eight microscopic stages used in this study are somewhat similar to those used by other Spanish mackerel researchers. Klima (1959) suggested using five stages, but only described macroscopic criteria. Powell (1975) described seven types of oocytes determined by microscopic analysis. However, he did not adequately relate these to whole gonad stages, and he did not include a stage recognizing pof's. Finucane and Collins (1986) named six gonad stages. However, they did not describe them in detail, did not provide any visual references, and did not include a stage for fish that have spawned at least once.

Macroscopic staging in Spanish mackerel is difficult, because subtle differences at the cellular level may not be manifested as distinct changes at the whole gonad level (Parrish et al. 1986). I found a low overall percent agreement when macroscopic stageing was compared with microscopic stageing and recommended a less detailed four stage system in an attempt to reduce error when only microscopic staging is done in the future.

Spawning Season, Spawning Location, and Nurseries

I found Spanish mackerel spawn in the Chesapeake Bay area from June to August, and that June is the peak spawning month. My findings agree with extensive, but general, observations from the late 1800's (Earll 1883/1887). Earll (1883), for example, found spawning fish in the Chesapeake Bay throughout the summer, starting in June, and he believed peak spawning was in July. Similarly, Hildebrand and Schroeder (1928) suggested that the spawning season occurred in late spring and early summer, but they did not state the exact months. Spawning occurs earlier south of the Chesapeake Bay area. Finucane and Collins (1986) found peak spawning off Georgia and the Carolinas in May and that spawning gradually declined over the rest of the summer. The fish that I collected in April from north Florida and Cape Hatteras, NC were not, however, ready to spawn. Presumably, my observations in these later areas reflects the fact that the beginning of the spawning season is asynchronous.

My findings of Gravid and, especially, Running Ripe females, suggest that Spanish mackerel spawn inside the Chesapeake Bay. The Running Ripe females I collected in the York River, and especially those further north at Mobjack Bay and Gwynn's Island, probably could not have moved outside the Bay to spawn, because those fish were only a few hours from spawning, if not already spawning. Where Spanish mackerel actually spawn in the Chesapeake Bay is not clear from gonad data, because they could move some distance before spawning. Plankton collections also provide little evidence of spawning areas, because modern collections in the Chesapeake Bay were made before the recent resurgence of Spanish mackerel, and they have not reported eggs of this species (Olney 1983). Despite these problems, my results agree with observations from the late 1800's, when Spanish mackerel were last abundant, that this species spawns in the Chesapeake Bay. Earll (1883), for example found "ripe" fish 40 miles inside the Bay, and Smith (1907) reported that the lower Chesapeake Bay was a "favorite" spawning ground. Spanish mackerel spawning grounds have also been difficult to locate elsewhere. Collins and Stender (1987), for example, attempted to describe larval distributions off the Southeast U.S. The few fish they collected were located nearshore, close to estuary mouths. Dwinell and Futch

(1973) made plankton surveys in the Northeastern Gulf of Mexico and suggested that spawning was widely distributed, but they collected few larvae and did not include estuarine waters in thier survey. The ten young collected in the Chesapeake Bay area by the VIMS surveys indicate Spanish mackerel use the area as a nursery. It also seems probable that these fish indicate survivorship of eggs and larvae north of Cape Hatteras, NC, but it is not clear where they were spawned. These fish, though small, are highly mobile and could have been either residents or transients in the areas where they were collected.

Sex Ratios

I found an overall sex ratio of 44% male and 56% female, but ratios varied greatly. These findings are new, because sex ratios have not previously been reported for Spanish mackerel. I found no trends by month or location, just a high degree of variability around a one to one ratio that could simply reflect segregation into spawning schools and/or difficulty in acquiring a sample of the population.

I found females generally dominated the catch in the larger sizes and grades, but there was no difference between the sexes for the smaller sizes. Reasons for the predominance of females at larger sizes could include: 1) faster growth in females than males, 2) higher mortality rates in males than females, and 3) more northerly migration by the larger females. The first two reasons are supported by Fable et al. (1987) who found females grow faster than males and live longer.

Length-at-Maturity

My estimates of size at first maturity, 230 mm FL for females and 232 mm for males, are slightly lower than those estimated for southern waters. Finucane and Collins (1986), the only previous estimates of size at first maturity, found L_{50} was 275-299 mm for both males and females off Georgia and the Carolina's. Powell (1975) found maturing oocytes in age I and II fish, but concluded that fish under age III (479 mean FL in his study) did not contribute substantially to the spawning population because, even though fish have begun to develop oocytes, they may not progress further and may not contribute to spawning biomass.

I found all females were mature at 330 mm FL and all males at 340 mm. These results are similar to, but again are slightly lower than reports from southern waters. Klima (1959) found all fish were mature by 350 mm FL off Florida.

Finucane and Collins (1986) found all males >350 mm FL and females >500 mm FL were mature in the Gulf of Mexico, but in the Atlantic all males >400 mm FL and females >425 mm FL were mature.

Batch Fecundity and Annual Fecundity

I found mean batch fecundity was 74,077 eggs and mean relative fecundity was 143 eggs/g female. Only two other reports exist on Spanish mackerel fecundity. Earll (1883) estimated a "batch fecundity" as 25,000 to 100,000 by counting all oocytes in the ovary at one time and Finucane and Collins (1986) estimated "fecundity" as 100,000 to 2,113,000 eggs by counting all oocytes greater than 0.2 mm diameter. It is not clear, however, what these studies really estimated, because both overlook the basic nature of a species with indeterminate fecundity. The problem with their approaches is that oocytes continually mature during the spawning season, so the standing stock of oocytes in an ovary is only some fraction of the total number spawned in a single season. These authors also did not differentiate the oocytes they counted into the different stages, and that omission makes it impossible to determine a batch fecundity, much less an annual fecundity which is the product of spawning frequency and batch fecundity (Hunter et al. 1985; Hunter et al. 1992). Earll's (1883) estimate of a "batch fecundity" , though similar to mine can not be used to estimate annual fecundity, because it is not clear what stage or stages of oocytes he counted. The same problem exists with Finucane and Collins' (1986) estimates of "fecundity".

Though important, I found it difficult and time-consuming to estimate batch fecundity in Spanish mackerel because: 1) Gravid ovaries are difficult to collect, because this transitory stage lasts only a few hours, 2) Gravid ovaries are delicate: if handled roughly ,hydrated oocytes may rupture from the follicles and lower fecundity estimates, 3) oocyte counting is time consuming: it took me 8-12 h to make 16 counts per fish using fresh ovaries, though Formalin preservation may reduce this time, and 4) all oocytes must have completed hydration to make accurate counts, so ovaries should not be included if hydration is not complete. I was not able to estimate fecundity by counting the most advanced stage of oocytes, an alternate approach (Hunter et al. 1985), for two reasons: 1) advanced oocyte stages can not be distinctly separated by size alone, and 2) some atresia was present at all times in the ovary. Because of the later phenomenon, fully yolked oocytes included in counts might really be resorbed instead of being spawned, and that would overestimate fecundity (Hunter et al. 1985; Barbieri 1994).

No study, including mine, has successfully estimated the spawning frequency of Spanish mackerel, though that is necessary to estimate annual fecundity in a multiple spawner (Hunter and Goldberg 1980; Hunter et al. 1985; Hunter and Macewicz 1985a). My attempts to collect Spanish mackerel using gill nets fished over a 24 hour period and, thereby, have known age pof's from which to use the pof method (Alheit et al. 1984; Goldberg et al. 1984) failed because I captured too few fish. Spanish mackerel apparently spawn often during the season, however, because I have observed fresh pof's in ovaries that had begun final oocyte maturation. Though not conclusive of spawning frequency that observation suggests that almost-daily spawns may be possible, a pattern reported in other multiple spawners including *Cynoscion regalis* and *Engraulis mordax* (Lowerre-Barbieri 1994; Hunter and Goldberg 1980).

General Discussion

I have determined that Spanish mackerel have been using the Chesapeake Bay area as a spawning ground in recent years and that they may also have been using it as a nursery for the young-of-the-year. That is the same pattern that occurred more than 100 hundred years ago (Earll 1883/1887; Chittenden, 1993b). Given the extent of the region, and depending on stock structure, spawning in the Chesapeake Bay region may contribute to an overall stock along the east coast of the U.S., if only during periods when this species is abundant north of Cape Hatteras. The broader question, why Spanish mackerel have again appeared in this area in large numbers (Chittenden et al. 1993b), still remains. Reproductive biology is only one aspect of the picture, and it is not yet clear how Spanish mackerel reproduction in the Chesapeake Bay affects the entire east coast population, if indeed there is only one population. Further questions concerning age-structure, year-class strength and migration patterns still need to be addressed for this region (Chittenden et al. 1993b). Until they are, it will be difficult to explain the recent period of resurgence. These problems with Spanish mackerel, in turn, are part of a still broader problem involving well-documented fluctuations in other species along the east coast of the U.S. (Chittenden, 1993b).

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