SEXUAL MATURATION AND SPAWNING OF ATLANTIC MENHADEN

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ABSTRACT

This study of the sexual development and incidence of spawning of the Atlantic menhaden, *Brevoortia tyrannus* (Latrobe), is based on an examination of ovaries collected along the Atlantic Coast of the United States from 1956 to 1959. Description of the distribution and developmental stages of ovarian ova was based on diameter measurements. Four developmental groups of ova were distinguishable in the ovaries of near-spawning fish: immature, intermediate, maturing and ripe. Two groups, each in a different stage of maturation, simultaneously developed but it could not be determined whether the second group was spawned.

A numerical relation, called the "ovary index," was established between the length of the fish and the weight of both ovaries and used to distinguish sexually active and inactive fish. Based on changes in the mean ovary index and numbers of sexually active fish in commercial catches, it was concluded that spawning occurred at different times in different areas of the coast. In the North Atlantic Area, spawning apparently took place during summer; in the Middle Atlantic Area, in spring and again in autumn; and in the South Atlantic Area, during winter.

Most females became sexually mature at age 2, and the estimated number of ova spawned by an individual each season ranged from 38,000 to 631,000 ova.

Seasonal variation in spawning was considered in relation to differential size and age distribution of the fish, seasonal migrations, and population structure.

The life history and biology of the Atlantic menhaden, *Brevoortia tyrannus* (Latrobe), are studied by the Bureau of Commercial Fisheries as part of a research program to determine causes of variations in the distribution, availability, and abundance of this species. Sexual maturation and spawning are among the more important aspects of the biology which must be understood to interpret such variations. Determination of the time and place of spawning not only may explain seasonal variations in the distribution and availability of adults, but is fundamental to a study of the distribution and survival of embryos and larvae. Knowledge of fecundity and of the size and/or age at first spawning may be used to assess the reproductive potential of the spawning stock.

The work had several aims: (1) to describe the macroscopic changes of ovarian ova as they develop to maturity, (2) to develop a method of determining rapidly and objectively the relative maturity of ovaries, (3) to investigate the distribution of near-spawning fish in time and space, (4) to determine the age and size at first spawning, and (5) to estimate the fecundity of fish of different sizes.

COLLECTION AND PRELIMINARY TREATMENT OF OVARIES

Most of the ovaries used in this study were obtained from routine length and age samples taken from purse seine catches landed throughout the fishing season at Portland, Maine; Gloucester, Mass.; Amagansett, N.Y.; Port Monmouth, N.J.; Lewes, Del.; Reedville, Va.; Beaufort-Morehead City, N.C., from 1956 to 1959 (fig. 1). Additional specimens were obtained from pound net catches landed at Port Monmouth and Reedville prior to commencement of the purse seine fishing season

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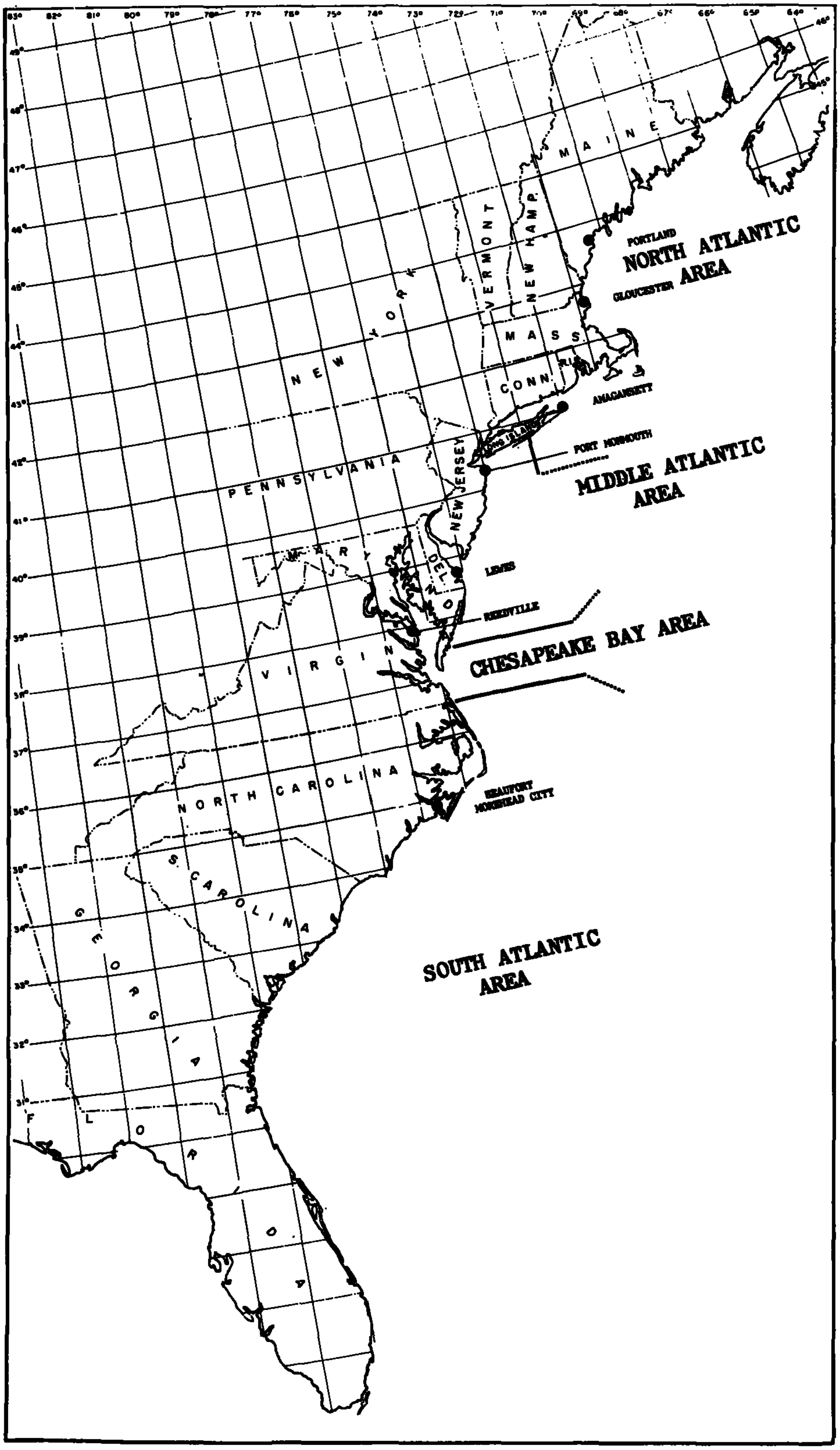

FIGURE 1.—Collection localities and areas used in summarizing maturity and spawning data on Atlantic menhaden.

and from incidental landings in various localities by otter trawlers. Methods of sampling the catch followed those described by June and Reintjes (1959).

At the time of collection, both ovaries were removed from each female, weighed to the nearest 0.1 g., and assigned an arbitrary stage of sexual maturity. In 1956 and 1957, ovaries of the first five females in each catch sample were labeled, wrapped in cheesecloth, and preserved in 10 percent formalin. Only those containing ripe ova were preserved in 1958 and 1959. Arbitrary stages of maturity assigned to ovaries in the field were:

Stage I. Ovaries small, torpedo-shaped, deep red, and occupying a small fraction of the body cavity. Ova invisible to the naked eye.

Stage II. Ovaries red to yellow, occupying about one-third to one-half of the body cavity. Ova invisible to the naked eye.

Stage III. Ovaries swollen, yellow, and occupying about two-thirds of the body cavity. Ova visible through the ovarian membrane.

Stage IV. Ovaries occupying about three-fourths or more of the body cavity. Ova yellow and readily separated from the follicles when the ovarian wall was pressed.

Stage V. Ovaries flabby, bloodshot, and occupying less than one-half of the body cavity. Intact, ripe ova present in the lumen of an ovary.

The primary purposes of examining ovaries and assigning arbitrary stages of maturity in the field were: (1) to insure collection and preservation of all ripe specimens (Stage IV), and (2) to distinguish recently spent specimens (Stage V), since after hardening in formalin, the latter usually were indistinguishable from those in the early maturing stage (Stage II).

Preserved ovary specimens collected in 1956 and 1957 were used for detailed study of maturation. Several specimens containing ripe ova which were collected and preserved in 1958 and 1959 also were used. Specimens length, and at least one specimen, when available, was chosen at random from each half-centimeter length class represented in the weekly catch samples at each port. This method of selection resulted in nearly equal representation of all length and age classes appearing in the catch samples during the 1956 and 1957 fishing seasons. Of 3,945 preserved specimens, 1,030 (26.1 percent) were used for detailed study. During the 1956–59 fishing seasons, ovaries of 37,548 females were examined in the field for determination of stage of maturity.

MEASUREMENT OF OVA FOR MATURITY DETERMINATIONS

The distribution and stages of relative maturity of ova within the ovaries were determined from diameter measurements. Since all preserved ova were not spherical, it was necessary to choose some arbitrary method of measuring their diameters. Two methods were compared. One hundred of the most mature ova in a single ovary first were measured along the axis which, by chance, was parallel to the graduations of an ocular micrometer. The same ova were then measured along the shortest and longest axes and the two measurements averaged (table 1). The variance of the mean of single measurements was 4.27 and of two measurements, 1.48. Single measurements, however, were made in one-third the time required for two measurements. Thus, for expediency, all ova subsequently were measured once along whatever axis fell parallel to the ocular micrometer

TABLE 1.—*Comparison of measurements of random diameters and the mean of maximum and minimum diameters of 100 ova from a single ovary (specimen 3.3583), in micrometer units* [1]

Random diameter	Mean diameter	Random diameter	Mean diameter	Random diameter	Mean diameter
35	33.0	31	31.5	34	34.0
33	33.0	31	34.0	33	34.5
34	34.0	34	35.0	32	33.0
35	35.0	39	24.5	35	35.5
38	34.5	35	34.0	37	36.0
36	35.5	32	34.0	39	36.0
32	32.5	34	35.5	37	35.5
32	35.0	33	34.5	36	34.5
33	33.5	38	35.0	33	36.5
34	35.0	35	34.5	37	35.5
33	34.5	38	36.5	37	34.5
39	36.0	35	36.0	33	34.0
34	34.C	36	35.0	35	35.0
34	24.5	34	35.0	34	33.5
37	35.5	33	32.5	38	33.0
33	33.0	38	36.0	31	34.0
34	34.0	34	33.5	33	34.5
33	34.0	35	34.5	32	34.0
35	32.5	34	36.0	34	32.0
35	35.0	36	36.5	35	34.0
30	33.0	33	31.5	37	35.0
31	32.5	30	34.5	36	35.5
32	32.5	37	35.5	33	34.5
34	31.5	35	35.5	39	36.5
33	32.0	35	36.0	32	35.0
33	32.5	36	35.0	35	34.0
32	33.5	36	35.0	35	34.0
35	33.0	34	36.5	35	34.0
34	33.5	32	34.5	36	36.0
35	33.5	32	34.0	34	35.0
32	32.5	34	33.5	35	35.0
33	33.5	35	35.5	37	34.5
35	34.0	35	34.0		
35	35.5	38	34.0		
Mean					34.49 | 34.36
Variance					4.27 | 1.48

[1] One micrometer unit equals 0.033 mm.

TABLE 2.—*Diameter-frequency distributions of maturing ova in samples from various locations within a single ovary (specimen 0.10812)*

[P=Periphery; M=Mid-section; I=Interior]

Diameter	Location								
	Anterior			Central			Posterior		
	P	M	I	P	M	I	P	M	I
Millimeters	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
0.73	2	2	2	1	----	2	----	1	1
.76	2	1	3	4	3	----	----	----	2
.79	1	5	5	9	8	5	3	7	3
.82	12	16	13	11	12	6	5	13	8
.86	10	12	19	22	15	23	16	16	16
.89	20	28	23	26	21	27	26	13	24
.92	27	34	40	22	21	36	22	24	29
.96	31	24	33	35	12	26	32	31	44
.99	28	21	30	19	36	40	35	34	31
1.02	19	13	13	15	11	17	19	25	18
1.06	14	6	7	4	12	17	12	9	9
1.09	4	7	2	2	5	4	7	5	9
1.12	5	1	2	3	2	1	2	3	3
1.16	1	2	2	4	4	1	5	3	2
1.19	----	2	1	----	2	2	1	1	2
1.22	----	----	----	----	----	----	1	3	----
1.25	----	----	----	----	----	----	1	----	----
Total	176	174	195	177	164	207	187	188	201
Mean diameters (mm.)	0.95	0.94	0.93	0.93	0.95	0.95	0.96	0.96	0.95
Weight of sample (g.)	.084	.088	.94	.088	.082	.092	.094	.084	.092

graduations. This method has been applied by other investigators (Clark, 1934; June, 1953; Schaefer and Orange, 1956; Yuen, 1955) and was judged to be sufficiently precise in the present study.

Different areas within a single ovary of a pair were sampled to determine if the maturing ova were distributed uniformly. A cross section, approximately 1 millimeter (mm.) thick, was cut from the anterior, central, and posterior parts and a wedge removed from each section. Each wedge was divided into three parts, corresponding to the periphery (*P*), mid-section (*M*), and interior (*I*), and a subsample of approximately 0.09 g. taken. Diameters were measured and counts were made of all maturing ova in each of the nine subsamples and the results (table 2) analyzed statistically. Neither the differences in mean diameters, nor the differences in numbers were significant at the 95 percent level.

Comparisons also were made of the mean diameters and numbers of mature ova in samples from the central portions of the right and left ovary (table 3). A *t*-test showed no significant difference in mean ova diameters; however, a statistically significant chi-square value ($P<0.01$) resulted from comparison of the numbers of ova. Inspection of the data showed discrepancies in the 0.82, 1.02, and 1.06 mm. size classes, but since the frequency distributions otherwise appeared similar, it was judged that there were no biological differences in ova from the right and left ovary.

TABLE 3.—*Diameter-frequency distributions of maturing ova in samples from the right and left ovary of a single fish (specimen 6.7012)*

Diameter	Right ovary	Left ovary
Millimeters	*Number*	*Number*
0.73	11	12
.76	11	21
.79	41	57
.82	94	146
.86	138	148
.89	204	219
.92	259	254
.96	255	249
.99	290	241
1.02	154	102
1.06	101	57
1.09	47	28
1.12	21	25
1.16	23	15
1.19	15	9
1.22	4	5
1.25	1	7
Total	1,669	1,595
Mean diameter (mm.)	0.95	0.93

Ova that were measured to establish the maturity stage of the preserved specimens were obtained by cutting a cross section from the central portion of the right ovary and removing a small wedge. The wedge was placed on a glass slide, and the ova were teased from the follicular tissues by dissecting needles with the aid of a binocular microscope. Parallel guidelines etched on the glass minimized the chance of measuring the same ovum more than once. Diameter measurements were made to the nearest ocular micrometer unit (0.017 mm.). If a specimen contained only immature ova (<0.18 mm.), measurements of about 100 ova were considered adequate to establish this stage of development. If larger ova were present, generally from 200 to 300 of the most mature ova were measured to delineate their size distribution.

DESCRIPTION OF THE OVARIES

Ovaries of Atlantic menhaden are paired, elongated organs suspended from the dorsal wall of the abdominal cavity by the mesovarium. They are elliptical in cross section and separate from each other, except where the two oviducts unite posteriorly before entering the cloaca. The right ovary usually is slightly larger than the left. Ovaries of sexually immature fish are deep red, torpedo-shaped, and may measure no more than several millimeters in length. They are similar in appearance to the testes, but are distinguishable by the oocytes which can be clearly seen under magnification, even in recently metamorphosed juveniles. As females develop to maturity, their ovaries increase in length and girth, and become firm and pale yellow. At the approach of spawning, the ovaries become distended, occupying two-thirds or more of the abdominal cavity; the peripheral blood vessels become enlarged; and the ova are visible through the ovarian membrane. Following spawning, the ovaries are flaccid and bloodshot, and residual ova occur in the follicular tissues and in the lumina.

DEVELOPMENTAL STAGES OF OVARIAN OVA

One or more distinct groups of ova are recognizable in the ovaries of an individual fish at one time or another throughout the year, depending on the proximity of spawning. Based on the appearance and diameters of formalin-preserved material, these may be described as follows:

Immature

Ova which are transparent, irregular in shape, and which contain relatively large, eccentric nuclei. These range from less than 0.02 mm. to approximately 0.22 mm. in diameter and average 0.11 mm. These are present in great numbers and comprise the oocytes from which smaller numbers of ova periodically mature (fig. 2).

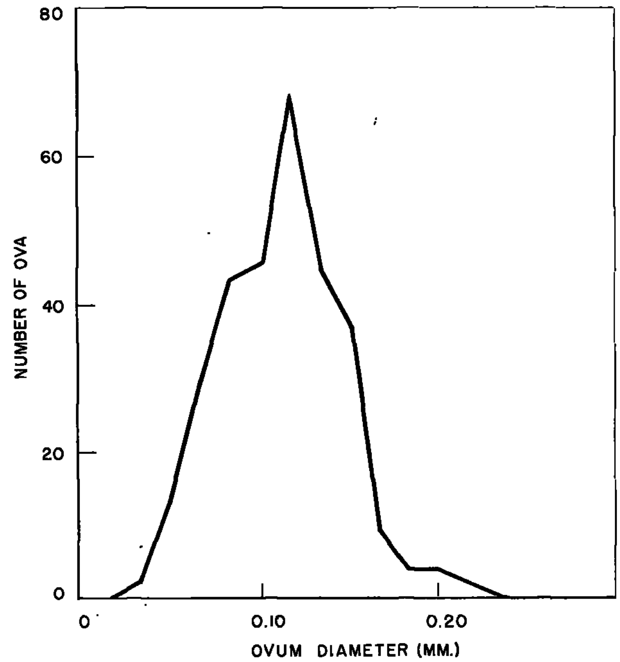

FIGURE 2.—Frequencies of ovum diameter of 300 immature ova from an Atlantic menhaden (specimen 2.1483).

Intermediate

Ova which are semiopaque, spherical, and in which the nuclei have become obscure due to the deposition of yolk granules in the cytoplasm. These range from approximately 0.18 to 0.34 mm. in diameter and are barely visible without magnification.

Maturing

Ova which are opaque and yellow due to abundant yolk material. These range from approximately 0.35 to 0.78 mm. in diameter and are clearly visible within the follicles.

Ripe

Ova which are translucent, each with a single, yellow oil globule, from 0.10 to 0.19 mm. in diameter. Ripe ova range from approximately 0.79 to 1.33 mm. in diameter. They readily burst from the follicles when the ovarian wall is pressed and sometimes are found lying loosely in the lumen of an ovary.

The four developmental groups of ova are present in the ovaries of all near-spawning fish. Development to maturity of ova within the ovaries of a single fish, with no connotation of time, is illustrated in figure 3. The percentage frequencies of ova-diameter measurements of several specimens were grouped into six arbitrary

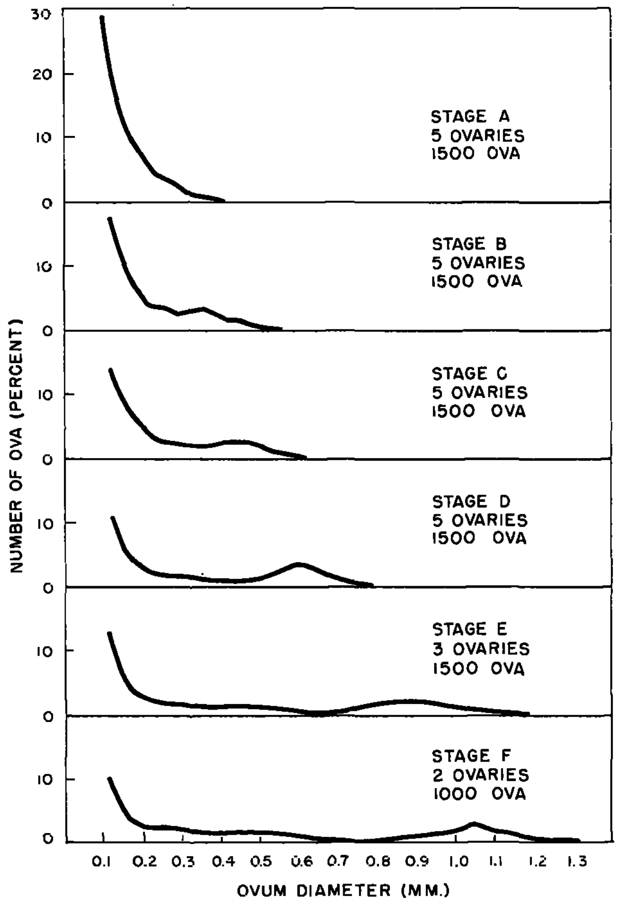

FIGURE 3.—Frequencies of ovum diameter showing the development to maturity. (The data were classified into six arbitrary stages according to the mode of the most mature group of ova. The smallest immature ova were not measured.)

stages, based on the mode of the most mature group, and smoothed twice by a moving average of three. Only ova larger than 0.12 mm. were included. A mode representing ova which eventually would ripen during a single spawning season was first discernible at 0.27 mm. (stage A). It became more sharply defined at 0.36 and 0.48 mm. (stages B and C) and distinct at 0.63 (stage D). The mode at approximately 0.90 mm. (stage E) represented semitranslucent ova which, on the basis of size, had become almost separated from the preceding groups. Ripe ova, ranging from 0.86 to 1.33 mm., with a mode at 1.08 mm. (stage F), constituted a distinct group and were nearly ready to be extruded. A second group of developing ova, between approximately 0.34 and 0.68 mm., was distinguishable by the time that the most advanced group became semitranslucent (stage E).

OVARY SIZE AS A MEASURE OF MATURITY

Many workers have used ova-diameter measurements to characterize the relative sexual maturity of the ovaries of individual fish (Brock, 1954; Clark, 1934; Thompson, 1915). This method, however, is laborious, and where large numbers of fish are examined, some simpler, objective method usually is desirable. Changes in ovary weight in relation to body size as the ovaries develop to maturity have been used in spawning studies on a number of species (Farran, 1938; Masterman, 1913a and 1913b; Olsen and Merriman, 1946). Later investigators (June, 1953; Schaefer and Orange, 1956; Yuen, 1955) related the size of ovarian ova to the weight of the ovaries and size of the fish and established indices of maturity which ultimately could be computed from ovary weight and fish size.

In the present study, the relation between ova diameters and an "ovary index" was examined in

TABLE 4.—*Ovary indices of 1,030 specimens containing ovarian ova in various stages of development*

Ovary index	Developmental stage of the most mature ovarian ova				Total
	Immature	Intermediate	Maturing	Ripe	
	Number	*Number*	*Number*	*Number*	*Number*
<1.0	150	16			166
1.0–1.9	145	202			347
2.0–2.9	12	82	2		96
3.0–3.9		14	6		20
4.0–4.9			42		42
5.0–5.9			39		39
6.0–6.9			31		31
7.0–7.9			46		46
8.0–8.9			28		28
9.0–9.9			19		19
10.0–10.9			21	1	22
11.0–11.9			20		20
12.0–12.9			24		24
13.0–13.9			16		16
14.0–14.9			9		9
15.0–15.9			18		18
16.0–16.9			14	1	15
17.0–17.9			18	2	20
18.0–18.9			7	1	8
19.0–19.9			13		13
20.0–20.9			9	1	10
21.0–21.9			6	1	7
22.0–22.9			3		3
23.0–23.9			2		2
24.0–24.9			3	2	5
25.0–25.9					1
26.0–26.9					
27.0–27.9			1		1
28.0–28.9					
29.0–29.9				1	1
30.0–30.9					
31.0–31.9					
32.0–32.9					
33.0–33.9					
34.0–34.9				1	1
Total	307	314	398	11	1,030

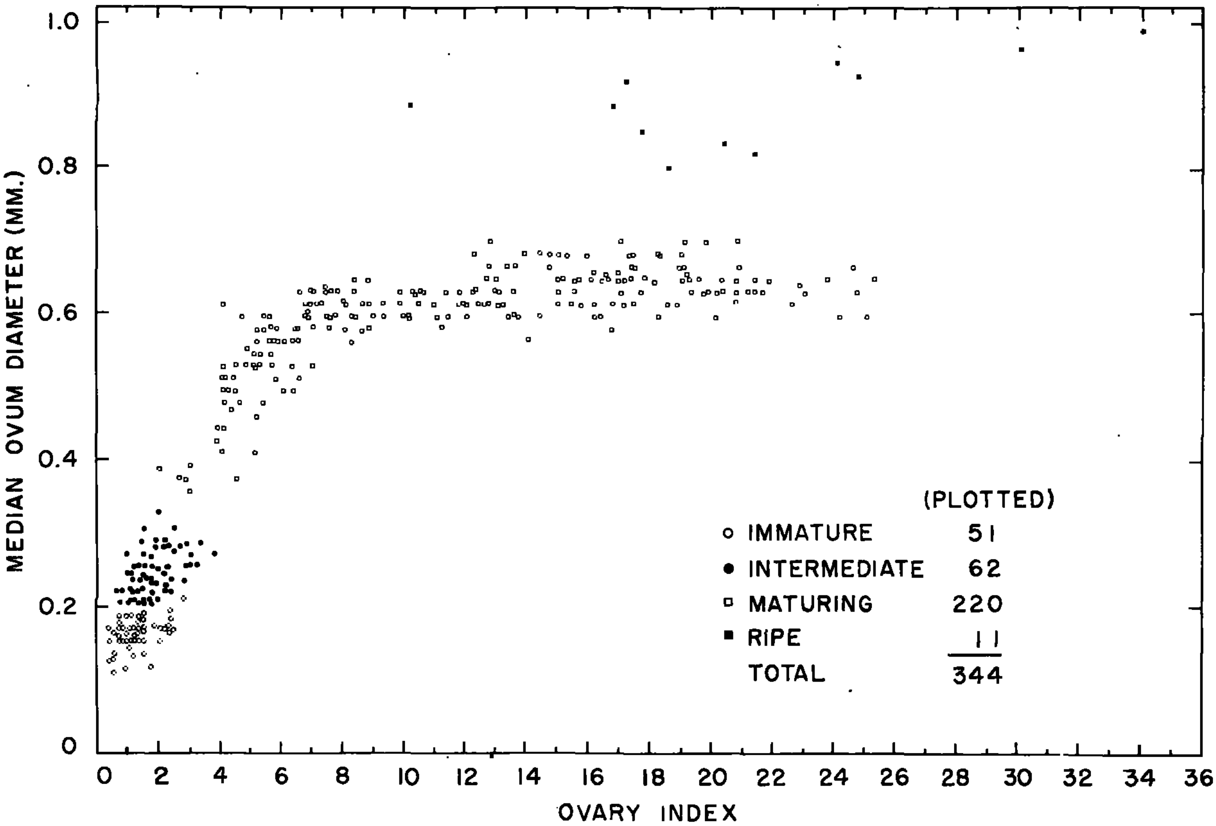

FIGURE 4.—Relation between ovary index and median of diameter frequency distributions of the most mature group of ova in 344 specimens.

1,030 specimens. The index was computed from the formula: $O.I.=\frac{W\times 10^7}{L^3}$

where $O.I.$=ovary index
W=weight of both ovaries in grams
L=fork length of the fish in millimeters [1]

Of 621 specimens which contained only immature or intermediate ova (<0.34 mm. in diameter), 607 (97.7 percent) had an ovary index of less than 3, and the remainder had an index of less than 4 (table 4). Indices of 409 specimens which contained maturing and ripe ova ranged from 2.9 to 34, and all but eight of these (2.0 percent) had an index greater than 4. In figure 4, the median of the ova-diameter frequency distributions of the most mature ova was plotted against the corresponding ovary index. The relation increased linearly up to an ovum diameter of about 0.60 mm., changed abruptly, and then tended to level off. The ovary index of 11 specimens which contained ripe ova, however, varied between 10 and 34, and there appeared to be a definite relation between the size of the most advanced ovarian ova and the ovary index.

From the foregoing, it was concluded that there was reasonably good agreement between the ovary index and the size of ovarian ova. Thus, the ovary index provided a simple, objective means of distinguishing ovary specimens which were approaching spawning. Since relatively few ripe and recently spent ovaries were found in the commercial catches, a more precise measure of sexual maturity was superfluous. Ripe ovaries were readily distinguishable by the fact that ova flowed freely from the oviduct with the slightest pressure on the ovaries. Recently spent ovaries also were easily distinguished by their flaccid, bloodshot appearance, and most of these yielded an ovary index of three or less. Verification was

[1] In Atlantic menhaden, body weight is nearly proportional to the cube of the length.

made by the presence of intact, ripe ova in the lumina of the ovaries.

PLACE AND TIME OF SPAWNING INFERRED FROM OVARY INDICES

The geographical and seasonal distribution of spawning was inferred from ovary indices on the assumption that females with an index of 4.0 or more would have actively spawned somewhere in the vicinity of capture. For convenience, those with an index of 4.0 or more were classified as "active" and those with an index of less than 4.0, as "inactive." Females with an index of less than 4.0 whose ovaries were hollow, flaccid, bloodshot, and contained some intact, ripe ova were classified as "spent." The resulting data were summarized by four major geographical areas described by June and Reintjes (1959) and shown in figure 1. The numbers of females classified according to the above criteria are listed by area, month, and year in table 5. In figures 5, 6, and 7 the percentage frequencies of sexually active females are shown

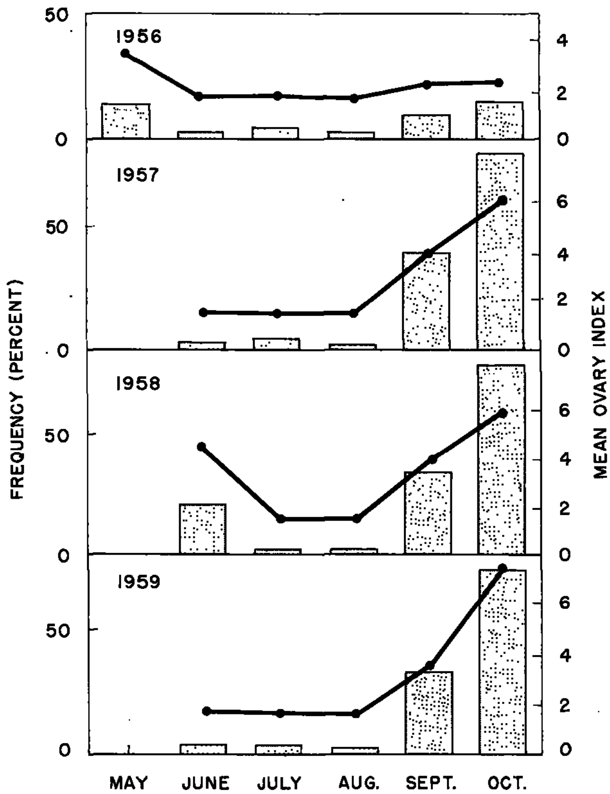

FIGURE 5.—Frequencies of sexually active females and mean ovary indices, by month and year, North Atlantic Area, 1956–59.

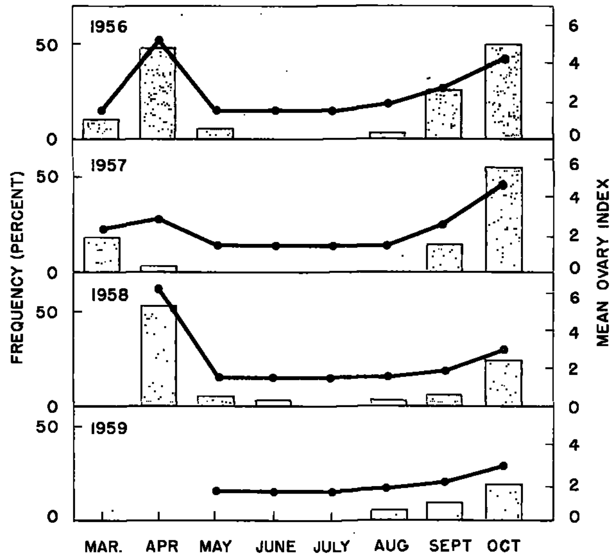

FIGURE 6.—Frequencies of sexually active females and mean ovary indices, by month and year, Middle Atlantic Area, 1956–59.

by month and year for the North, Middle, and South Atlantic Areas. The mean ovary index also is plotted on these figures.

Because so few ripe and recently spent specimens were collected (only 11 specimens containing numerous ripe ova were encountered in the routine field examination of several hundred thousand fish during 4 years of sampling), it was not possible to determine the time required for ova of sexually active fish to become fully ripe and extruded. Hence, it is possible that spawning occurred in some locality other than where sexually active females were caught. The paucity of both ripe and recently spent specimens and the occurrence of numerous collections which consisted entirely of sexually active females suggests, however, that Atlantic menhaden change their habits so as to become unavailable to the fishery prior to and following spawning. Whether spawning fish segregate in schools or in smaller groups is unknown.

NORTH ATLANTIC AREA

Atlantic menhaden were caught by purse seines in northern coastal waters from June to October in every year; consequently most of our collections were limited to this period. A few specimens were obtained from pound nets in May 1956. Ovaries of 6,511 females were ex-

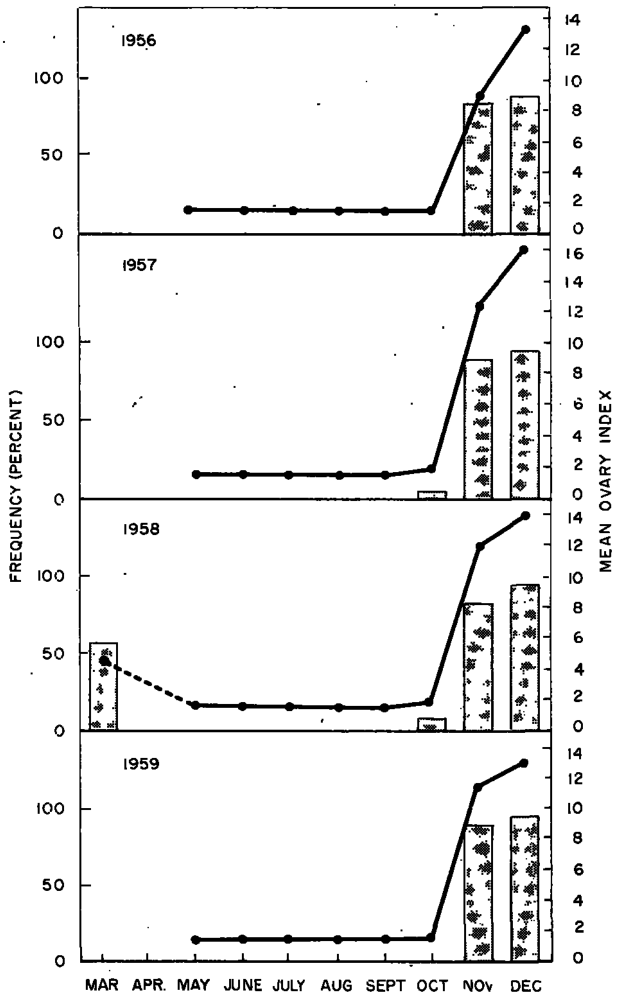

FIGURE 7.—Frequencies of sexually active females and mean ovary indices, by month and year, South Atlantic Area, 1956–59.

amined between 1956 and 1959. Active and/or spent females were represented in every month for which there were data (table 5 and figure 5). Many of the specimens obtained in May 1956 and in June 1958 were active and had high ovary indices. In most years, however, the numbers of active fish in June, July, and August constituted only a small fraction of the monthly totals, and the mean ovary index increased in September and reached a maximum in October. It was concluded from these data that spawning took place in the North Atlantic during the entire period that the fish were available to the fishery, and reached a peak in October.

The above conclusions agree with published reports of the occurrence of planktonic eggs and larvae. Kuntz and Radcliffe (1917) found both eggs and larvae in the vicinity of Woods Hole, Mass., in June, July, August, and again in October. Herman (1959) reported the occurrence of eggs and larvae in Narragansett Bay from May to August and again in October and concluded that there was a split spawning season in that locality, the autumn spawning being the most productive. Perlmutter (1939) reported eggs and larvae in northern Long Island waters from May to September, and Richards (1959) and Wheatland (1956) concluded that spawning took place in Long Island Sound from May to October, with peaks occurring in early summer and in autumn.

MIDDLE ATLANTIC AREA

A pound net fishery for Atlantic menhaden operates off New Jersey and southern Long Island beginning in April and is followed by the purse seine fishery beginning in May. The purse seine fishery continues until October when the fish disappear from the coastal waters (June and Reintjes, 1959). Except during mild winters, when occasional catches are made by pound nets and otter trawls, the fish are not known to occur in concentrations inshore until the following March or April.

Ovaries of 14,749 females were examined from March to October during the 4-year period (a few specimens were obtained in December 1957). Active and spent females occurred in substantial numbers in April, but abruptly decreased in May (table 5 and figure 6). Only 12 active or spent females appeared in the catches in June, July, and August. In every year, the number of active fish increased in September and generally reached a maximum in October. The mean ovary index was high in April, remained low during the summer, but increased again in September and October. It appears from these data that spawning occurred in spring and again in autumn, with possibly very limited spawning during the summer. The main spawning season was indicated to be in autumn.

There are no published reports of the occurrence of planktonic eggs and larvae within the area; however, evidence that spawning takes place in spring and autumn comes from numerous plankton collections of larvae taken at Indian River Inlet, Del. Routine sampling was conducted at this location

TABLE 5.—*Number of sexually inactive, active, and spent female Atlantic menhaden in catch samples, by area and month, 1956–59*

Area, year, and ovary condition	Month										Total
	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
North Atlantic:											
1956:											
Inactive				323	671	573	200	102			1,869
Active			6	2	22	8	22	29			89
Spent			36	11	21	43	12	53			176
1957:											
Inactive				199	600	494	128	19			1,440
Active				4	16	9	91	135			255
Spent					1	3	2	12			18
1958:											
Inactive				65	285	299	166	18			833
Active				19	2	1	98	84			204
Spent					9		17	3			29
1959:											
Inactive				279	427	418	235	17			1,376
Active				8	17	9	106	75			215
Spent				5		2					7
Subtotal:											
Inactive				866	1,983	1,784	729	156			5,518
Active			6	33	57	27	317	323			763
Spent			36	16	31	48	31	68			230
Middle Atlantic:											
1956:											
Inactive	1	144	429	865	484	590	286	211			3,010
Active	1	218	1			1	92	213			526
Spent	9	94	67	4			3	1			178
1957:											
Inactive		61	205	765	813	757	407	281		9	3,298
Active	5	37	1				51	337			431
Spent	24	138	22				1				185
1958:											
Inactive		6	179	576	765	810	794	70			3,200
Active		61	9	4		3	24	21			122
Spent		52	25	2							79
1959:											
Inactive			137	813	984	1,056	549	108			3,647
Active						4	46	23			73
Spent											
Subtotal:											
Inactive	1	211	950	3,019	3,046	3,213	2,036	670			13,155
Active	6	316	11	4		8	213	594			1,152
Spent	33	284	114	6			4	1			442
Chesapeake Bay:											
1956:											
Inactive		32	316	369	438	370	156	39			1,720
Active											
Spent											
1957:											
Inactive		310	79	346	436	434	329	156			2,090
Active		2									2
Spent											
1958:											
Inactive			35	428	430	256	374	110			1,633
Active											
Spent											
1959:											
Inactive			72	455	495	448	479	272	39		2,260
Active											
Spent											
Subtotal:											
Inactive		342	502	1,598	1,799	1,508	1,338	577	39		7,703
Active		2									2
Spent											
South Atlantic:											
1956:											
Inactive			359	446	424	524	230	188	52	38	2,261
Active									273	251	524
Spent											
1957:											
Inactive			385	473	339	178	101	80	40	10	1,606
Active								4	276	204	484
Spent											
1958:											
Inactive			279	300	241	93	210	61	39	44	1,267
Active	50							4	186	316	556
Spent	38										38
1959:											
Inactive			262	371	246	213	81	45	33	15	1,266
Active									243	347	590
Spent											
Subtotal:											
Inactive			1,285	1,590	1,250	1,008	622	374	164	107	6,400
Active	50							8	978	1,118	2,154
Spent	38										38

from 1955 to 1961 as part of an estuarine study conducted by the Menhaden Program. Neither eggs nor larvae were taken in July, August, and September. Larvae appeared in the collections in October, increased in number thereafter, and generally reached a peak of abundance in January. The smallest larvae occurred in the October samples. Their length increased in November, but thereafter remained relatively constant until April when both smaller and larger larvae occurred in the collections (Pacheco, Unpublished Ms.).[2] These findings suggest the following hypotheses: (1) following a period of no spawning in the area throughout the summer, spawning begins in September or October; (2) larvae from the autumn spawning increase in length through November, but subsequently do not grow appreciably until April or May; and (3) smaller larvae which appear in the collections in April result from a spring spawning in the area, while the larger larvae represent the progeny from the previous autumn spawning. The occurrence of sexually active fish in autumn, their absence in the coastal waters during winter, and their reappearance in spring support these hypotheses.

CHESAPEAKE BAY AREA

In Chesapeake Bay, Atlantic menhaden are caught in quantity by pound nets beginning in April (McHugh, 1960). The purse seine fishery begins in late May and usually continues through October, at which time most of the fish apparently disappear from the Bay (June and Reintjes, 1959). Of 7,705 females examined between April and November, only two active specimens were found, both in April 1957 (table 5). No spent females were found. It was concluded, therefore, that spawning probably did not occur in Chesapeake Bay during the period considered.

Kuntz and Radcliffe (1917) were of the opinion that there were two spawning seasons in the Chesapeake Bay area, but offered no data to support their belief. Hildebrand and Schroeder (1928) reported that females with "well-developed" (although not ripe) ovaries were taken in autumn and that larvae were caught from January to April. These authors concluded that spawning occurred in autumn. Pearson (1941) obtained "a limited number" of eggs in late summer and several 20–24 mm. larvae in April and May plankton samples taken in lower Chesapeake Bay and concluded that some spawning probably occurred outside the area of collection during the winter. McHugh, Oglesby, and Pacheco (1959) found no fully mature fish in samples from pound net and purse seine catches, although some specimens approaching maturity were observed in early spring.[3] They further reported that no eggs were found in numerous plankton hauls in Chesapeake Bay; however, larvae 24 to 30 mm. in length were taken as early as April and appeared in greatest abundance in late April and early May. Massmann, Norcross and Joseph (1962) obtained larvae from November to May during monthly offshore plankton cruises in Virginia waters. The smallest specimens were taken in November and ranged between 7 and 10 mm. Those taken during the winter months were fairly uniform in size and ranged from 12 to 29 mm., while those taken in May were larger and ranged between 25 and 33 mm.

The foregoing evidence supports the present conclusion that spawning does not occur in Chesapeake Bay. It is probable that the larvae reported within Chesapeake Bay resulted from an autumn and winter spawning offshore.

SOUTH ATLANTIC AREA

In the South Atlantic Area, Atlantic menhaden are caught exclusively by purse seines, generally from May to December or January.[4] The summer fishery apparently is based on local stocks and usually lasts from about mid-May to mid-October (June and Nicholson 1964). In November, large, migratory schools appear off the coast of North Carolina and support an intense fishery until mid-December when they disappear off Cape Fear, N.C. (June and Reintjes, 1959).

Examination was made of 8,592 specimens obtained from the purse seine fishery and from incidental catches made by otter trawlers. No active females appeared in the catches from May to September in any year, and only eight active females were found in October (table 5 and figure 7). With the appearance of migrating schools in

[2] Catches of postlarval Atlantic menhaden, *Brevoortia tyrannus*, at Indian River, Delaware. Unpublished Manuscript, U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C.

[3] While no sexually active fish were found in the present study from 1956–59, specimens examined in 1955 showed the presence of 1 sexually active fish in May, 1 in September, and 22 in October. Only inactive fish were found in June, July, and August.

[4] Catches in January consist almost exclusively of young-of-the-year fish (age 0) which are sexually immature. These were excluded from the study.

November and December, the number of active females increased abruptly. Eighty-nine percent of the females examined in November and 95 percent of those examined in December were active. The particularly high ovary indices in November and December also indicated that most of the females in the fishable population were in spawning condition. Among 88 specimens collected on an exploratory fishing cruise in March 1958, 50 were active and 38 were spent.

Reintjes (1961) reported the occurrence of eggs and/or newly hatched larvae, principally in the vicinity of Capes Fear and Lookout, N.C., and Cape Kennedy, Fla., from November to March, but none were found during other months of the year. Based on the known distribution of adults, he believed those taken off the North Carolina coast were Atlantic menhaden, while those taken off central Florida were Atlantic menhaden or yellowfin menhaden (*B. smithi*).

Corroborative evidence of continuous spawning off the North Carolina coast from late fall to early spring is furnished from routine plankton collections taken in the vicinity of Beaufort, N.C., from 1955 to 1961 (Unpublished data, Menhaden Program, Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C.). Eggs and larvae have been collected in the ocean only during the late fall and winter months; however, eggs have not been taken at any time in samples at Beaufort Inlet. In every year, larvae appeared in Beaufort Inlet samples beginning in November or early December, were present continuously thereafter until early or mid-April, and reached a peak of abundance in late February or early March. Larvae in the early December samples invariably were small, ranging from approximately 10 to 20 mm. in length. Samples throughout the winter contained mixed sizes, indicating successive waves of spawning in nearby waters. The largest larvae usually occurred in the April samples. Larvae were never taken from May to November.

It was concluded that spawning occurred in the South Atlantic Area from mid-November to late March, with a peak probably occurring sometime in mid-winter. Based on the concentrations of sexually active fish and the abundance of newly hatched larvae, it is likely that waters off the North Carolina coast are one of the major spawning grounds for Atlantic menhaden.

AGE AND LENGTH AT FIRST MATURITY

Females were considered immature if their ovaries were in the inactive stage (ovary index <4.0) and ova remnants were not found in the follicular tissues or in the lumina. Fish whose ovaries were either active (ovary index>4.0) or in the spent stage, with intact, ripe ova present in the lumina, were considered sexually mature. On the basis of these criteria, little difficulty was experienced in distinguishing sexually mature individuals.

No sexually active age-0 fish (June and Roithmayr, 1960; June and Reintjes, 1959) were found. This age group, therefore, was not considered further. In most years a few mature females of age 1 occurred in catch samples in the Middle Atlantic Area in October; nine females, ranging from 240 to 265 mm. in length, were found in 1956; two, 215 and 235 mm., in 1957; and one, 210 mm., in 1959 (table 6). Greater numbers were found during the fall fishery in the South Atlantic Area. Between October and December (table 7), 22 mature females, ranging from 205 to 260 mm., were found in 1956; one 190-mm. specimen in 1957; 52 specimens, ranging between 180 and 280 mm., in 1958; and two specimens, 200 and 205 mm., in 1959. No mature females in this age group were found in samples from other areas in any year. From these data, it was concluded that some Atlantic menhaden attained maturity at age 1, and these ranged from approximately 180 to 280 mm. in length. The mean lengths indicate that there was a size difference at which females reached maturity in the two areas. There also was a tendency for the mature females

TABLE 6.—*Relation of age, length, and spawning condition of Atlantic menhaden, Middle Atlantic Area, September and October, 1956–59*

Year and age group	Inactive			Active		
	Number	Fork length		Number	Fork length	
		Range	Mean		Range	Mean
		Millimeters	*Millimeters*		*Millimeters*	*Millimeters*
1956:						
Age 1	158	195–265	225.2	9	240–265	248.4
Age 2	127	235–300	260.7	121	235–305	263.2
1957:						
Age 1	339	185–255	209.2	2	215–235	225.0
Age 2	306	195–305	253.7	98	210–320	266.6
1958:						
Age 1	0	----	----	0	----	----
Age 2	838	215–280	248.4	43	250–280	264.2
1959:						
Age 1	437	165–230	194.3	1	210	210.0
Age 2	91	210–280	241.5	23	235–285	257.6

TABLE 7.—*Relation of age, length, and spawning condition of Atlantic menhaden, South Atlantic Area, October–December, 1956–59*

Year and age group	Inactive			Active		
	Number	Fork length		Number	Fork length	
		Range	Mean		Range	Mean
		Millimeters	*Millimeters*		*Millimeters*	*Millimeters*
1956:						
Age 1	270	140–230	169.3	22	205–260	232.5
Age 2	3	200–235	220.0	100	225–305	265.0
1957:						
Age 1	66	150–210	182.9	1	190	190.0
Age 2	58	180–220	196.4	121	185–315	279.8
1958:						
Age 1	135	170–280	198.1	52	180–280	217.4
Age 2	9	195–240	212.2	253	185–300	261.5
1959:						
Age 1	75	130–225	160.7	2	200–205	202.5
Age 2	9	185–250	210.6	114	210–290	259.0

of age 1 to be the larger individuals within the age group in both areas.

In every year, mature females of age 2 were found in catch samples in the Middle and North Atlantic Areas beginning in September. By October, 48 percent of all females in this age group examined during the 4-year period had attained maturity, and these ranged between 225 and 320 mm. in length. In the South Atlantic Area, 97 percent of the females examined from October through December during the 4-year period were mature, and these ranged from 195 to 315 mm. in length. Thus it would appear that most females mature by age 2. All females of age 3 and older ages were found to be mature. Ovaries of the latter age groups which were examined microscopically, without exception, contained ova remnants from a previous spawning. These findings, in general, agree with those of Westman and Nigrelli (1955) who stated that all females at age 3 and some at age 2 appeared to be mature.

FREQUENCY OF SPAWNING DURING A SEASON

The frequency distribution of ova diameters in figure 3 showed that, within the ovaries of Atlantic menhaden, there was a progression to maturity of one group of advanced ova, distinguished by a single, well-defined mode. This was followed by a second group of developing ova which became clearly discernible by the time the mode of the first group had advanced to about 0.90 mm. In the lower three panels of the figure (stages D–F), it may be seen that ova constituting the second group continued to increase in size as the first group advanced to maturity. Thus, it appears that at least two groups of ova develop within a single spawning season, but the question arises as to whether the second matures and is spawned in the same season.

Because so few females in a ripe or near-ripe condition were available in the fishable population, there was no way of determining the fate of the secondary group of ova. A few specimens were collected which had high ovary indices and contained intact, ripe remnants in the lumina. These ovaries were turgid, contained numerous near-ripe ova, and appeared to be ready to spawn in the near future. Recently spent ovaries contained relatively few intermediate and maturing ova in the follicular tissues. Furthermore, the yolk granules of intermediate and maturing ova which remained in the follicular tissues of recently spent ovaries collected in spring were speckled, and the ova were dark, distorted, and appeared to be disintegrating. Yolk granules of the numerous developing ova in specimens taken in late summer and early autumn were globular, and the ova were spherical (cf. Intermediate ova, p. 259). Finally, the absence of remnants within follicular tissues in latent ovaries of sexually mature fish during the summer indicates that residual intermediate and maturing ova are not carried over to the following spawning season. From available evidence, it is impossible to decide conclusively the frequency of spawning by individual fish. We favor, however, the hypothesis of the maturation and fractional spawning of more than one group of ova during a single season.

NUMBER OF OVA SPAWNED

The number of ova assumed to be extruded from the most advanced group of ovarian ova was estimated for 38 fish which ranged in length from 203 to 346 mm. A sample from each ovary specimen was weighed to the nearest 0.001 g. Ova were teased from the follicular tissues and those classified as maturing (p. 259) were counted. The number of maturing ova in both ovaries was estimated by multiplying the number in the sample by the ratio of the weight of both ovaries to the weight of the sample (table 8). The number of ova per female varied widely, but increased with length. Individual estimates ranged from 38,000 to 631,000 ova. A plot of the estimated number

TABLE 8.—*Estimated number of ova in the most advanced group in ovaries of fish of different sizes*

Fork length	Fish weight	Weight of both ovaries	Sample weight	Number of maturing ova in sample	Estimated number of maturing ova in pair of ovaries
Millimeters	*Grams*	*Grams*	*Gram*		*Thousands*
203	167	7.1	0.179	1,266	50
204	157	7.3	.178	1,439	59
208	174	6.9	.159	1,036	45
211	174	6.8	.174	1,292	50
216	184	5.6	.189	1,295	38
221	221	12.3	.205	1,525	92
228	234	15.2	.182	1,348	113
240	269	14.5	.237	1,161	71
243	281	19.4	.283	1,642	113
244	280	10.3	.232	1,299	58
246	290	15.5	.222	1,261	88
247	283	7.3	.278	1,852	49
251	295	25.4	.209	1,113	135
258	327	23.6	.290	1,967	160
259	322	14.2	.217	1,715	112
267	346	32.6	.196	1,383	230
270	368	26.3	.165	1,278	204
274	443	41.9	.216	1,135	220
278	368	27.6	.279	1,788	177
278	446	45.1	.113	793	316
285	441	35.2	.412	2,753	235
285	413	37.1	.161	1,194	275
290	536	42.3	.292	2,005	290
299	572	39.9	.118	1,230	416
305	619	54.0	.194	1,485	413
309	661	44.8	.346	2,546	330
313	543	50.0	.189	921	244
313	579	41.1	.356	2,665	308
317	646	62.8	.142	977	432
317	651	46.6	.173	1,012	272
327	750	40.2	.167	1,208	291
328	637	55.4	.334	3,452	573
333	732	74.3	.102	594	433
336	771	68.9	.206	1,536	514
339	910	62.8	.183	1,071	368
343	848	89.0	.174	1,042	533
345	858	78.9	.194	1,551	631
346	786	81.5	.209	1,438	561

of ova on fish length (figure 8) gave a relation which is curvilinear.

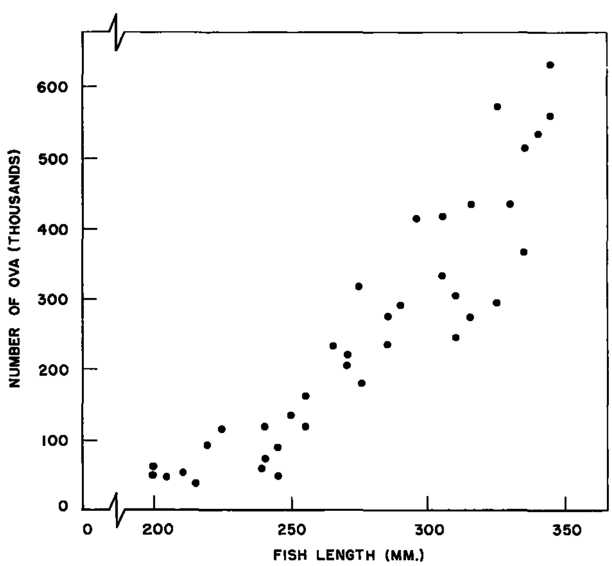

FIGURE 8.—Relation between fish length and the estimated number of maturing ova.

Suttkus and Sundararaj (1961) reported on the fecundity and reproduction of Gulf menhaden, *B. patronus*. This species reaches maturity younger and at a smaller size than *B. tyrannus*. The number of ova produced, for fish of comparable size, is greater in the former species.

DISCUSSION

The seasonal variations in spawning in different areas of the coast may be explained by seasonal variations in the distribution of age and size classes of fish. June (1961), June and Nicholson (1964), and June and Reintjes (1959 and 1960) have shown that during the summer, the purse seine catch in the North Atlantic Area is composed mostly of age-3 and older fish, whereas fish of ages 1 and 2 dominate the catches in other areas. Since all females were found to be sexually mature at age 3, it would be expected that any spawning during the summer would be limited to the North Atlantic Area. Based on the occurrence of dominant length-age groups, June and Nicholson (1964) postulated a cyclic north-south migration of at least a portion of the population north of Chesapeake Bay—southward in autumn and northward in spring. Such a migration pattern would account for the occurrence of the older, sexually mature fish (many of which are in spawning condition) in the Middle Atlantic Area in September and October and again in March, April, and May, and probably accounts for the appearance of sexually mature fish (most of which are in spawning condition, p. 259) in the South Atlantic Area in November and December. Apparently not all fish migrate southward in autumn, however, since numerous inactive and recently spent females occurred in the catches in the North and Middle Atlantic Areas in September and October (table 5). They also are known to have occurred in the latter area during the winter, yet very few inactive, and no spent females appeared in the catches in the South Atlantic Area in November and December. Although the time required for sexually inactive ovaries to become active is unknown, it seems unlikely that maturation would occur over a period of about 2 weeks—the time interval between the disappearance of schools from surface waters in the Middle Atlantic Area and the reappearance of schools off the North Carolina coast. The almost complete absence of inactive females among the older, sexually mature fish which appear in large schools in the latter area in November and December would suggest that the southward migration in autumn is primarily a spawning migration.

The hypothesis of a cyclic north-south migration of spawning fish would explain the observed variations in the time and space distribution of sexually active fish, eggs, and larvae. According to this hypothesis, spawning during the summer is restricted to the North Atlantic Area where older, sexually mature fish are largely confined. Beginning in September, there is an increase in the number of active fish followed by a general movement southward during which spawning occurs. These migrating schools are joined by other sexually active fish in the Middle Atlantic Area, and spawning continues as the schools move southward. In some seasons, these large schools of sexually active fish are followed as far southward as Delaware and northern Maryland by the purse seine fleet, and the appearance of eggs and larvae in the coastal waters of Delaware and Virginia (p. 265) coincides with the occurrence of such schools in these latitudes. Eventually the schools disappear from the surface waters (sometime in late October), but reappear several weeks later off the coast of North Carolina. Spawning occurs in the South Atlantic Area through the winter. Some individuals continue spawning during the return northward migration in spring as both sexually active and recently spent specimens appear along with sexually inactive specimens in pound net catches along the Middle Atlantic coast in March, April, and May. The older, sexually mature fish finally return to the summer grounds north of Long Island, N.Y. Thus, it is possible that those fish which were sexually inactive in the previous autumn, and which may not have joined in the southward migration, spawn in northern waters during the summer.

The above hypothesis also could account for the variation in meristic characters of juvenile Atlantic menhaden inhabiting estuarine nurseries reported by June (1958) and Sutherland (1963). These authors found that juveniles of five successive year classes were separable into two groups or subpopulations, one occurring north and the other south of Long Island. They also showed that variations in meristic numbers were associated with seasonal differences in water temperatures on the spawning grounds, and Sutherland concluded that the relative stability of the meristic pattern suggested genetic origin. Our data suggest that the fish which spawn in waters north of Long Island in summer constitute a distinct group, which becomes segregated from that which migrates southward and spawns in the South Atlantic Area in winter. If this is indeed the case, it is likely that differences in the physiological condition of individuals, hence differences in the time of year at which their gonads develop to spawning, have a genetic basis. It also would be expected that some overlap in spawning would occur in the vicinity of Long Island where individuals of these two spawning groups apparently segregate in autumn and intermingle again in the following spring during the return migration into northern waters.

Variations in fecundity of females of comparable size (fig. 8) and age suggest that differences in the size and age at attainment of sexual maturity (p. 266) should be explored further, since these may yield further insight into the question of genetic differences in physiology between these two apparent spawning groups. Along these lines, further study of spawning fish in Florida waters is necessary to determine if they differ from those farther northward.

SUMMARY

Ovaries of Atlantic menhaden (*Brevoortia tyrannus*) were obtained during routine sampling of catches at seven ports along the Atlantic Coast of the United States during four fishing seasons, 1956–59. Ovaries were weighed and examined at the time of sampling. Some were preserved for further laboratory study.

Preliminary studies indicated that diameter-frequency distributions of ova sampled in different parts of a pair of ovaries were similar. One or more developmental groups of ova were distinguishable within the ovaries, depending on the nearness of spawning; these were immature, intermediate, maturing, and ripe. Plots of ova-diameter frequency distributions showed the simultaneous development of more than one group of ova within the ovaries of an individual fish.

A relation, called the "ovary index," was calculated between fish length and the weight of both ovaries and compared to the medians of the diameter frequency distributions of the most mature group of ova in 1,030 specimens. Although

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the ovary index did not completely correct for the effect of fish length on the weight of ovaries containing ova in the same stage of development, it could be used reasonably well to distinguish inactive ovaries from those which were advancing toward spawning.

Time of spawning in four geographical areas was inferred from ovary indices. Spawning apparently occurred in the North Atlantic Area from May to September; in the Middle Atlantic, from March through May and again in September and October; and in the South Atlantic, from October through March. There was little evidence that spawning occurred inside Chesapeake Bay.

Few females were found to be mature at age 1 (180–280 mm., fork length); most were mature at age 2 (195–320 mm., fork length); and all were mature at age 3 (over 200 mm. fork length).

Simultaneous maturation of two groups of ova within the ovaries suggests that an individual female may spawn more than one group of ova during a single season; however, no conclusions were reached since there was no way of determining the fate of the secondary group. Extrusion of ova appears to be fractional.

Assuming that ova comprising the most advanced group are extruded, estimates of the number of ova spawned during spawning season, ranged from 38,000 to 631,000, depending on the length of the fish.

Variation in times and places of spawning and attainment of first maturity appear to be related to the differential distribution of age and size groups, seasonal migrations, and population structure.

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