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Comparison of Vertebral Counts of Atlantic Menhaden

by Fred C. June

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ABSTRACT

Comparison was made of vertebral counts of 6,048 adult Atlantic menhaden (Brevoortia tyrannus) collected in three localities along the Atlantic coast of the United States to determine if autumn and spring spawners were distinguishable by this meristic character. Two discrete groups of spawners were identified: one occurring in Cape Cod and Long Island waters in spring and the other in Long Island and North Carolina waters in autumn. The mean vertebral count of spring spawners was 46.914 and of autumn spawners, 47.031. Lower mean counts of spring spawners in 3 successive year classes were shown to be similar to those of juveniles of the same year classes occupying estuarine nurseries north of Long Island, while higher mean counts of autumn spawners were similar to those of juveniles occurring south of Long Island. The consistency of mean vertebral counts of spring and autumn spawners for 3 consecutive years suggests that the observed differences are of genotypic origin.

INTRODUCTION

Investigation of the population structure forms one phase of a program of research on the Atlantic menhaden (Brevoortia tyrannus). The purposes of this phase of research are to identify any natural biological units within the population and to determine the overlap in time and space between them. Thus far, morphological characters of juveniles have been compared (June, 1958; Sutherland, 1963) and the distribution of spawning (Higham and Nicholson, 1964; Reintjes, 1961) has been studied.

The above-mentioned studies have helped to formulate hypotheses regarding population structure, but there still are many unanswered questions. Some of the more important questions concern the relationship of spring and autumn spawners. When adults appear inshore near Long Island, N.Y., and northward in April or May, some are in spawning condition (spawners), but the majority may be classified as "spent", or otherwise sexually inactive (nonspawners). The proportion of spawners decreases through summer, but increases again in September and reaches a maximum in October (Higham and Nicholson, 1964). Prior to their disappearance from northern waters in October, spawners and nonspawners congregate in large schools. These schools move southward during November and congregate off the North Carolina coast until mid-December (June and Nicholson, 1964). Before or during the southward migration, however, the composition of the schools changes, for among the adult fish, only spawners appear off North Carolina, and catches consisting of nonspawners sometimes are taken in Long Island waters immediately before and following the southward migration of spawners. Except for rare appearances, fish are absent from inshore waters through winter. In the following April or May, they reappear inshore, and mixed groups of spawners and nonspawners again occur from Long Island northward (Higham and Nicholson, 1964).

The purpose of this study was to see if a comparison of mean vertebral counts would show a relationship between (1) spawners and nonspawners that appear together from Long Island northward in April and May, (2) spring and autumn spawners in that locality, (3) autumn spawners in that locality and off North Carolina, and (4) spring and/or autumn spawners in those localities and the juvenile stocks in adjacent estuarine nurseries.

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MATERIALS AND METHODS

Fifty-two samples of adult Atlantic menhaden, comprising 6,048 specimens, were collected in spring (April-May) from pound net catches in the vicinity of Cape Cod, Mass., and Long Island, N.Y., and in autumn (October-December) from purse seine catches near Long Island, N.Y., and Beaufort, N.C., from 1957 to 1960 (fig. 1). Collecting was limited to periods when spring or autumn spawners occurred in the catches in greatest numbers. Incidental catches of Atlantic menhaden by pound nets provided the earliest and only available samples in spring. Adverse weather, which delayed the setting of pound nets in waters north of Long Island during April and May, thwarted attempts to secure a greater number of samples in the Cape Cod area. Although efforts were made to obtain at least 100 specimens in each sample, early season pound net catches sometimes failed to provide sufficient numbers. Also, some of the preserved material was lost during storage because of decomposition, separation of vertebral columns, and dissociation of identifying labels. Individual samples available for study contained from 41 to 313 specimens.

At the time of collection, fish were examined for sex and maturity. Most gonads were weighed, and, following the general method of Higham and Nicholson (1964), males and females with a "gonad index" of 4.0 or more were classified as spawners and those with an index of 3.0 or less as nonspawners. Fish which were in spawning condition in April and May were classified as "spring spawners", those in spawning condition from October to December as "autumn spawners."

The fork length of each fish, in centimeters, was recorded and a scale sample taken, following the methods described by June and Reintjes (1959). The vertebral column, including the skull and most of the caudal fin, was removed, labeled, and preserved in 10 percent formalin.

Counts of vertebral numbers were made from radiographs (Sutherland, 1958) and included all vertebrae between, but not including the occipital bone and the hypurals (June, 1958; Sutherland, 1963). Abnormal vertebrae (found in 0.4 percent of the fish examined) were counted if distinguished by a suture between fused centra, or by the presence of a neural or haemal spine. Columns in which individual vertebrae could not be distinguished were discarded (three specimens). Ages were determined from scales, and the fish were assigned to year classes as defined by June and Roithmayr (1960).

The correlation between vertebral counts and fish length was tested for significance. Vertebral counts were subjected to the variance-ratio and Bartlett's tests to test the assumption of common variance, and an analysis of variance was used to test the significance among means of sexes, age groups, year classes, spawning groups in the same and different localities, and juveniles and adults from adjacent localities (Snedecor, 1956).

Table 1 summarizes data on length, age, and vertebral count of 6,048 spawners and nonspawners in samples by locality and date. Means and sums of squared deviations used in the analyses also are given.

RESULTS

Variation of Vertebral Counts With Fish Length

To determine whether vertebral counts were related to fish length, a correlation analysis was made of the individual and combined samples from each locality (spawners and nonspawners were treated separately). Three of the correlation coefficients were of borderline significance (at the 5 percent level), and the maximum variation attributable to length in combined samples was suggested to be less than 2 percent. Accordingly, length was not considered in the analyses which follow.

Variation between Sexes

Because of unequal numbers of males or females in some samples, differences in the mean vertebral counts between samples from the same locality might reflect differences between the sexes. However, analysis of mean vertebral counts of 12 samples, comprising 859 individuals of 3 separate year classes (1955, 1956, and 1957), showed that none of the samples had a statistically significant difference between sexes. It was concluded that variation associated with sex was random, a conclusion which agrees with the findings of June (1958) and Sutherland (1963) concerning juveniles. Accordingly, males and females were not separated in subsequent analyses.

Variation of a Year Class with Age

In all localities, the proportion of fish of a given year class in samples changed as the year class became older. Accordingly, heterogeneity between mean vertebral counts could arise from the varying numbers of fish at different ages in the samples. Comparisons, therefore, were made of the two most abundant year classes (1955 and 1956) at successive ages in each locality (table 2). Of the 12 possible comparisons (samples which contained no fewer than 60 fish of a given age), one showed a significant difference at the 5 percent level, and this was confined to nonspawners of the 1955 year class in the Long Island samples. In this case, there was a small decrease in the mean vertebral count

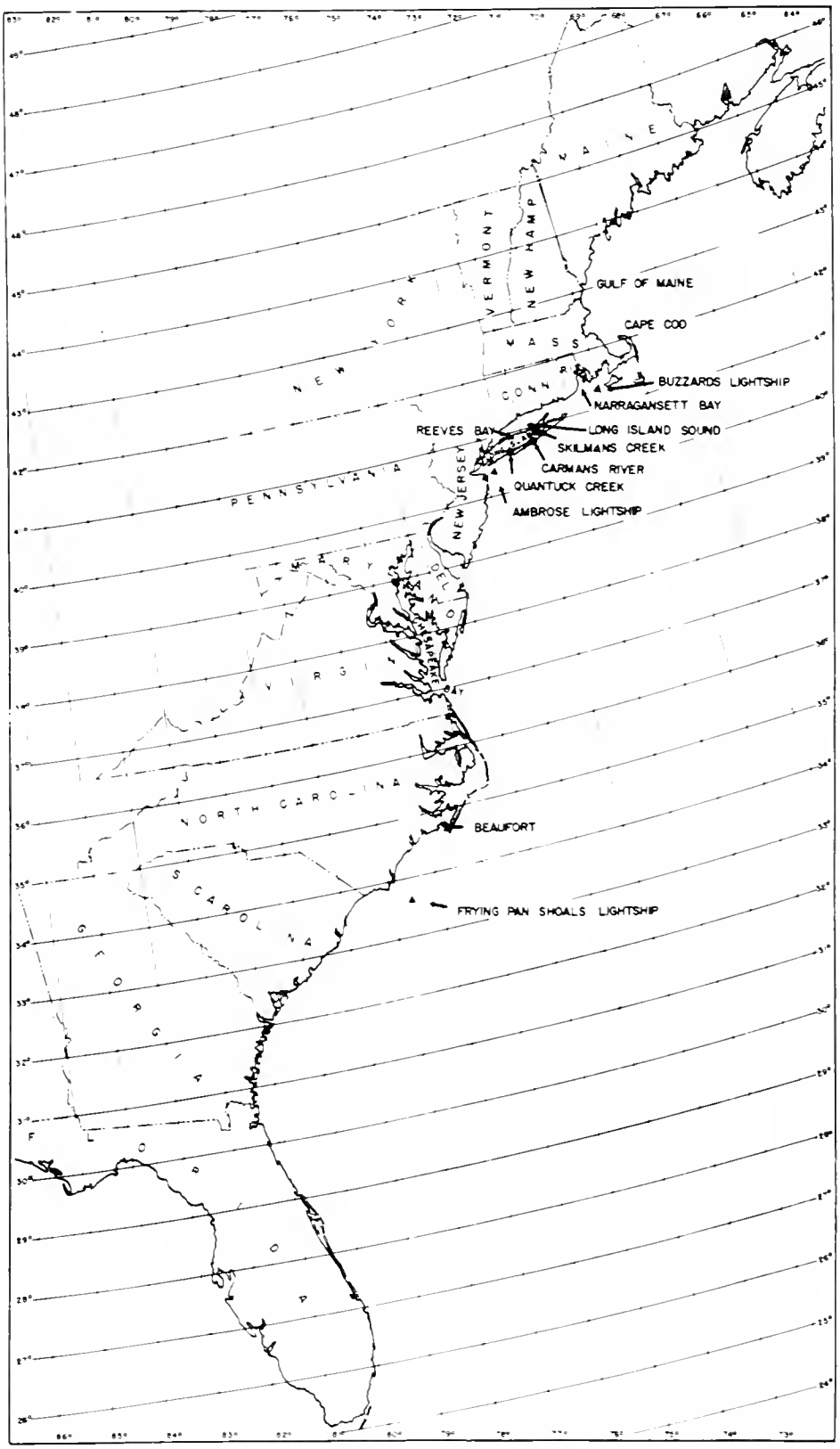

Figure 1.--Map of the Atlantic coast of the United States showing locations mentioned in the text.

Table 1.--Fork lengths, ages, and vertebral counts of Atlantic menhaden in samples from three localities along the Atlantic coast of the United States, 1957-60

Locality and date	Length			Age			Vertebrae							
	Range	Average	Fish in sample	Range	Average	Fish in sample	45	46	47	48	49	Average	Fish in sample	Sum of squared deviation from the average
	Cm.	Cm.	Number	Years	Years	Number	Number	Number	Number	Number	Number	Number	Number	
Cape Cod, Mass.:														
Spring spawners:														
May 19-25, 1958[1].	30.0-36.3	33.4	101	4- 9	6.2	70	1	13	70	5	--	46.888	89	20.876
May 17, 1959.....	24.3-34.3	30.3	264	2- 8	4.7	248	2	59	179	22	--	46.844	262	82.584
May 16-17, 1960..	22.7-34.6	30.4	208	3- 9	4.8	205	1	38	151	16	1	46.894	207	59.662
Total.....	22.7-36.3	30.3	573	2- 9	--	523	4	110	400	43	1	46.869	558	163.122 164.450
Nonspawners:														
May 19-25, 1958..	29.1-35.7	33.0	121	3- 9	5.9	103	--	15	85	15	--	47.000	115	30.000
May 17, 1959.....	24.7-34.5	30.5	290	3- 8	4.6	281	--	29	224	37	--	47.028	290	65.779
May 16-17, 1960..	23.0-34.4	29.4	313	2- 8	4.2	309	--	38	229	46	--	47.026	313	83.796
Total.....	23.0-35.7	--	724	2- 9	--	693	--	82	538	98	--	47.022	718	179.575 179.644
Long Island, N.Y.:														
Spring spawners:														
Apr. 12-14, 1958.	26.6-35.8	31.2	63	3-10	5.6	61	--	11	47	5	--	46.905	63	15.429
Apr. 16, 1958....	29.4-36.2	32.1	49	3-10	5.7	48	--	8	37	3	--	46.896	48	10.479
Apr. 17-18, 1958.	28.3-35.2	31.7	137	3-10	5.4	134	2	31	90	12	--	46.830	135	47.082
Apr. 19, 1958....	28.2-34.7	31.8	59	2- 8	5.1	38	1	9	43	4	--	46.877	57	16.140
Apr. 21, 1958....	29.3-35.9	32.0	75	3- 8	5.4	75	--	9	55	9	--	47.000	73	18.000
Apr. 22, 1958....	27.8-34.7	31.6	155	3- 8	5.3	154	--	21	110	21	--	47.000	152	42.000
Apr. 23, 1958....	28.5-35.9	31.6	142	3-10	5.5	136	3	21	97	21	--	46.958	142	53.746
Apr. 24, 1958....	28.4-35.0	31.9	51	3- 8	5.8	50	--	5	41	4	--	46.980	50	8.980
Apr. 21, 1959....	27.4-35.4	32.4	100	3- 9	6.0	99	--	12	77	11	--	46.990	100	22.990
Apr. 22, 1959....	28.4-35.2	32.7	100	3- 8	6.3	99	--	17	72	11	--	46.940	100	27.640
Apr. 23-24, 1959.	26.2-35.2	32.1	200	3- 9	5.8	199	--	27	151	22	--	46.975	200	48.875
Apr. 25, 1959....	25.6-35.7	32.2	100	3- 8	5.7	100	--	17	74	9	--	46.920	100	25.360
Apr. 19-21, 1960.	26.2-36.2	31.5	213	3- 9	5.7	209	--	47	147	17	--	46.858	211	59.735
Total.....	24.6-36.2	--	1,444	2-10	--	1,402	6	235	1,041	149	--	46.932	1,431	396.456 401.289
Nonspawners:														
Apr. 16, 1958....	27.4-36.0	31.4	51	3- 9	5.0	50	--	9	39	3	--	46.882	51	11.294
Apr. 17-18, 1958.	28.2-35.7	31.4	63	3-10	5.2	62	--	4	50	9	--	47.079	63	12.603
Apr. 19, 1958....	27.7-34.1	31.3	41	3- 7	4.9	23	--	4	31	6	--	47.049	41	9.902
Apr. 21, 1958....	29.0-34.4	31.5	73	3- 9	5.1	72	--	10	46	12	--	47.029	68	21.941
Apr. 22, 1958....	27.9-34.9	31.2	90	3- 9	5.1	90	1	13	65	8	--	46.920	87	24.437
Apr. 23, 1958....	27.9-36.0	31.4	158	3- 9	5.2	154	--	17	127	14	--	46.981	158	30.943
Apr. 24, 1958....	29.0-34.4	31.9	64	3- 9	5.7	64	--	9	44	9	--	47.016	61	16.984

[1] Inclusive dates given for accumulated pound net catches.

Table 1.--Fork lengths, ages, and vertebral counts of Atlantic menhaden in samples from three localities along the Atlantic coast of the United States, 1957-60--Continued

Locality and date	Length			Age			Vertebrae							
	Range	Average	Fish in sample	Range	Average	Fish in sample	45	46	47	48	49	Average	Fish in sample	Sum of squared deviation from the average
	Cm.	Cm.	Number	Years	Years	Number	Number	Number	Number	Number	Number	Number	Number	
Nonspawners--Cont.														
Apr. 27, 1959.....	28.3-34.8	31.6	100	3- 8	5.1	100	--	8	83	7	1	47.010	99	18.990
Apr. 28, 1959.....	26.5-33.8	30.6	100	3- 8	4.3	100	--	11	64	24	--	47.131	99	33.293
Apr. 29, 1959.....	26.3-35.5	31.1	100	3- 9	5.1	99	--	10	75	14	--	47.040	99	23.838
Apr. 30, 1959.....	25.6-34.9	29.7	100	3- 8	4.0	100	--	6	73	21	--	47.150	100	24.750
May 1, 1959.....	24.5-33.6	28.7	100	3- 8	4.0	98	--	11	71	17	--	47.061	99	27.636
Apr. 19-21, 1960..	26.9-34.7	30.7	272	3- 8	4.9	267	--	31	203	37	--	47.022	271	67.867
														324.478
Total.....	24.5-36.0	--	1,312	3-10	--	1,279	1	142	971	181	1	47.030	1,296	329.826
Autumn spawners:[2]														
Oct. 6, 1958.....	25.6-33.8	30.0	84	--	--	--	--	6	64	13	1	47.107	84	22.036
Oct. 8, 1958.....	25.1-33.0	27.9	98	--	--	--	--	13	77	8	--	46.949	98	20.745
Oct. 9, 1958.....	26.6-33.7	30.1	76	--	--	--	--	6	57	10	--	47.055	73	15.781
Oct. 13, 1958.....	26.2-33.9	29.0	68	--	--	--	--	5	54	9	--	47.059	68	13.765
Oct. 14, 1958.....	25.9-32.4	27.5	84	--	--	--	--	6	63	15	--	47.107	84	20.036
														92.363
Total.....	25.1-33.9	--	410	--	--	--	--	36	315	55	1	47.052	407	93.916
North Carolina:														
Autumn spawners:														
Nov. 14, 1957.....	25.2-34.3	30.8	111	2- 7	3.9	102	--	18	76	15	--	46.972	109	32.918
Nov. 18, 1957.....	27.8-33.7	31.1	100	2- 7	4.4	100	--	8	79	13	--	47.050	100	20.750
Nov. 22, 1957.....	26.6-33.7	30.5	134	2- 7	4.0	133	--	12	100	22	--	47.075	134	33.254
Nov. 27, 1957.....	26.7-33.7	30.7	100	2- 7	4.1	100	--	12	73	14	--	47.020	99	25.960
Dec. 16, 1957.....	27.2-33.5	30.5	100	2- 6	3.9	100	--	9	80	11	--	47.020	100	19.960
Nov. 17, 1958.....	26.0-34.6	30.2	100	2- 7	3.2	99	--	18	63	17	1	47.010	99	38.990
Nov. 18, 1958.....	26.9-35.0	31.3	100	2- 7	3.8	100	1	12	74	13	--	46.990	100	28.990
Dec. 1, 1958.....	22.6-35.3	30.4	200	2- 7	3.6	198	--	26	144	30	--	47.020	200	55.920
Dec. 2, 1958.....	24.0-33.8	27.5	100	2- 6	2.4	99	--	8	79	13	--	47.050	100	20.750
Dec. 4, 1958.....	23.5-33.1	27.8	100	2- 7	2.3	97	--	11	80	9	--	46.980	100	19.960
Nov. 30, 1959.....	24.4-33.5	29.0	100	2- 7	3.0	100	--	10	76	13	--	47.030	99	22.909
Dec. 1, 1959.....	26.8-34.7	30.3	100	2- 8	3.5	98	--	8	73	18	--	47.101	99	24.990
Dec. 2, 1959.....	26.3-34.4	29.9	100	2- 8	3.5	100	--	12	69	18	--	47.061	99	29.636
Dec. 8, 1959.....	25.8-33.7	29.0	100	2- 8	3.0	98	--	9	78	13	--	47.040	100	21.840
Dec. 9, 1959.....	24.3-35.1	28.1	100	2- 6	2.9	100	1	6	82	11	--	47.030	100	20.910
														417.737
Total.....	22.6-35.3	--	1,645	2- 8	--	1,624	2	179	1,226	230	1	47.030	1,638	419.534

[2] Some collections and all scale samples lost during storage.

Table 2.--Comparison of mean vertebral counts of Atlantic menhaden of the 1955 and 1956 year classes at successive ages

Locality	Year class	Mean vertebrae at age				Vertebrae difference between ages		
		2	3	4	5	2-3	3-4	4-5
		Number	Number	Number	Number	Number	Number	Number
Cape Cod:								
Spring spawners...	1955	--	--	46.833	46.851	--	--	-0.018
	1956	--	46.843	46.954	--	--	-0.111	--
Nonspawners.....	1955	--	--	47.000	46.933	--	--	.067
	1956	--	47.050	47.050	--	--	.000	--
Long Island:								
Spring spawners...	1955	--	--	46.930	46.921	--	--	.009
	1956	--	46.800	46.900	--	--	-.100	--
Nonspawners.....	1955	--	47.028	47.112	46.930	--	-.084	[1] .182
	1956	--	47.092	47.062	--	--	.030	--
North Carolina:								
Autumn spawners...	1955	47.011	47.000	47.093	--	0.011	-.093	--
	1956	47.041	47.062	--	--	-.021	--	--

[1] P is less than 0.05.

between ages 4 and 5, but in remaining comparisons the differences showed no consistent trend.

The significant decrease with age in mean vertebral count of nonspawners of the 1955 year class in the Long Island samples may be due to (1) differential mortality as the fish became older, (2) a shift in the spawning cycle of individual fish with advancing age, or (3) chance. Because the difference in the mean vertebral count between ages was significant only in the 1955 year class in one locality, it is unlikely that this source of variation altered the results of subsequent tests.

Variation between Year Classes

Samples from the different localities included fish of more than one year class. Therefore, if mean vertebral counts of the various year classes represented in the samples differed significantly, the mean counts of samples simply might reflect differences in age composition.

In every instance except one (nonspawners, Long Island) mean counts of both spawners and nonspawners of the 1956 year class were slightly higher than those of the 1955 and 1957 year classes (table 3). Differences as great as 0.145 vertebra are shown for mean counts between year classes (1956 and 1957 year classes in Cape Cod samples); however, no difference was statistically significant.

Table 3.--Comparison of mean vertebral counts of Atlantic menhaden of the 1955-57 year classes

Locality	Mean vertebrae for year class			Maximum difference in vertebrae
	1955	1956	1957	
	Number	Number	Number	Number
Cape Cod:				
Spring spawners...	46.841	46.905	46.760	0.145
Nonspawners.....	46.973	47.050	47.016	.077
Long Island:				
Spring spawners...	46.923	46.906	--	.017
Nonspawners.....	47.083	47.080	47.000	.083
North Carolina:				
Autumn spawners...	47.022	47.052	47.037	.030

Sutherland (1963) found the mean vertebral counts of juveniles of the 1956 year class significantly higher than those of the 1957, 1958, and 1959 year classes. Examination of daily and mean monthly surface water temperatures and salinities (Bumpus, 1957; Day, 1959a, 1959b, 1960) at lightship and shore stations along the Atlantic coast showed no striking anomalies during the period of early development of eggs and larvae in 1956. There was no pattern of correlation between the vertebral counts and the hydrographic data. An explanation of this phenomenon may involve one or more of the following points: (1) selection by spawning fish of temperature and/or salinity strata other than the surface waters considered, (2) variations in the time and place of spawning, (3) differential survival in the early life history stages, and

(4) differential genotypic variation between year classes.

Since differences between the mean vertebral counts of three year classes were not significant, variation between year classes was not considered in the following analyses.

Comparison of Spawners and Nonspawners within and between Localities.

The first major hypothesis tested in this study was that the spawners and nonspawners, which occurred together in Cape Cod and Long Island waters in spring, constituted two discrete groups of fish. Vertebral counts of spawners from each of the two localities first were tested for evidence of significance between sample means. Results of these analyses gave no indication of heterogeneity within localities. Further analysis indicated that spawners from the two localities probably were drawn from a homogeneous population. Similar comparisons of nonspawners, both within and between localities, led to the same conclusions. Accordingly, the vertebral counts of spawners from the two localities were pooled and compared with the pooled counts of nonspawners from both localities. A highly significant F value of 47.74 ($P_{0.01} = 6.64$) indicates that it is unlikely that the samples of spawners and nonspawners collected in Cape Cod and Long Island waters in spring were members of a homogeneous population.

Vertebral counts of 1,989 spawners ranged from 45 (10 fish) to 49 (1 fish), with the majority having 47 vertebrae (1,441 fish); mean counts of samples varied from 46.830 to 47.000. Vertebral counts of 2,014 nonspawners also ranged from 45 (1 fish) to 49 (1 fish), with most having 47 vertebrae (1,509 fish); mean counts of samples ranged from 46.882 to 47.150. The difference between the grand means of spawners (46.914) and nonspawners (47.027) was 0.113 vertebra.

The foregoing findings led to the second major hypothesis, namely, that the nonspawners which occurred in Cape Cod and Long Island waters in spring and the spawners which occurred in Long Island and North Carolina waters in autumn constituted a homogeneous population.

Mean counts of samples within each locality were tested for homogeneity and showed no significant differences in either locality. The autumn spawners from Long Island and North Carolina were then compared and gave no indication of heterogeneity. Finally, both groups of autumn spawners were compared with the nonspawners taken in Cape Cod and Long Island waters in spring, and differences were not significant.

Vertebral counts of 407 autumn spawners from Long Island ranged from 46 (36 fish) to 49 (1 fish), with most having a count of 47 (315 fish); mean counts of samples ranged between 46.949 and 47.107. A total of 1,638 autumn spawners from North Carolina had counts ranging from 45 (2 fish) to 49 (1 fish), with the majority having 47 (1,226 fish); mean counts of samples varied from 46.972 to 47.101. The grand means for Long Island and North Carolina autumn spawners were 47.052 and 47.030, respectively, as compared with a count of 47.027 for nonspawners taken in Cape Cod and Long Island waters in spring.

Finally, comparison was made of the mean vertebral counts of spring spawners and autumn spawners (nonspawners taken in Cape Cod and Long Island waters in spring were included with autumn spawners from Long Island and North Carolina). As might be expected, results of the analysis showed highly significant heterogeneity between the means ($F = 69.22$; $P_{0.01} = 6.64$). The grand mean vertebral count for 1,989 spring spawners was 46.914 and for 4,059 autumn spawners, 47.031, a difference of 0.117 vertebra.

The conclusions drawn from the foregoing analyses of vertebral counts were that (1) spring spawners in Long Island and Cape Cod waters constituted a homogeneous group which was distinct from nonspawners, (2) autumn spawners in Long Island and North Carolina waters and nonspawners in Long Island waters in spring (autumn spawners) constituted a homogeneous group, and (3) spring and autumn spawners constituted two discrete groups of fish. The term group is used here, as defined by Marr (1957), to describe "a fraction of a population with distinctive characteristics, the nature of which (phenotypic or genotypic) has not yet been determined."

Comparison of Juveniles and Spawners of the Same Year Class

From a study of mean vertebral counts, June (1958) and Sutherland (1963) found that juvenile Atlantic menhaden inhabiting estuarine nurseries along the Atlantic coast were separable into two groups--one occurring north of Long Island, N.Y., and the other south of there. Of further interest in the present study, therefore, is a comparison of the mean vertebral counts of spring and autumn spawning adults of a given year class with juveniles of the same year class (age 0) from these two general nursery areas to determine if some relationship could be established.

In table 4, the mean vertebral counts of spring spawners in three year classes (1955-57) are compared with the mean counts of juveniles of the same year class at age 0 from estuarine nurseries north of Long Island, and autumn spawners with juveniles from estuarine nurseries south of Long Island. Of six possible comparisons, all but two (both

Table 4.--Comparison of mean vertebral counts of juvenile Atlantic menhaden (age 0) from estuarine nurseries north and south of Long Island, N.Y., with spring and autumn spawners (older ages combined), respectively, of the same year class

Year class	Mean vertebrae					
	Juveniles north of Long Island (age 0)	Spring spawners (older ages combined)	Difference	Juveniles south of Long Island (age 0)	Autumn spawners (older ages combined)	Difference
	Number	Number	Number	Number	Number	Number
1955.....	46.666	46.889	[1] 0.223	47.083	47.022	[2] 0.061
1956.....	46.658	46.959	[1] .301	47.090	47.052	[2] .038
1957.....	46.645	46.760	.115	47.014	47.037	.023

[1] P is less than 0.01.
[2] P is less than 0.05.

involving the 1957 year class) were found to differ significantly (two were significant at the 5 percent level and two at the 1 percent level). Differences between means ranged from 0.023 (1957 year class, autumn spawners) to 0.301 (1956 year class, spring spawners). In four of the comparisons, there were increases in the mean vertebral counts with age; in two, decreases.

In most cases, there were statistically significant differences between the mean vertebral counts of juveniles of a given year class (age 0) inhabiting estuarine nurseries north and south of Long Island, and spring and autumn spawners of the same year class, respectively, occurring in an adjacent ocean locality. It is, however, evident that the mean counts of spawners and of juveniles in the respective localities followed a similar pattern; that is, lower mean counts were associated with spring spawners and juveniles occurring north of Long Island, and, conversely, higher counts with autumn spawners and juveniles occurring south of Long Island. The observed differences between juveniles and adults could have resulted from (1) changes in mean vertebral counts with age as mentioned in an earlier section, (2) recruitment of larvae into estuarine nurseries from ocean spawning grounds other than where spawners were collected, and (3) inadequate sampling of the spawning and/or juvenile populations within the respective localities.

DISCUSSION

In our studies of the Atlantic menhaden population structure, we are concerned with whether observed differences between groups of fish (for example, spring and autumn spawners) reflect discrete natural biological units within the population. Probably the most that we can hope to do through morphological studies is to gain some insight into the consistency of quantitative differences between groups of fish. Such information would lead to a better understanding of population structure.

Results of studies by June (1958) and Sutherland (1963) revealed consistent differences in mean vertebral counts (as well as other meristic characters) of juveniles in five successive year classes (1955-59) inhabiting estuaries north and south of Long Island. Juveniles identifiable with both groups were shown to be living together in Long Island estuaries. June (1958) found differences in meristic counts of juveniles in Long Island estuaries associated with fish length and hypothesized that the differences reflected the intermingling of progeny from autumn and spring spawnings. Sutherland (1963) noted that fish length was a possible source of variation within samples, but did not consider it in the analysis of his data. Examination of his raw data (table 5) reveals, however, that classification of individual samples from Long Island waters, as to northern or southern groups, also can be made on the basis of length. Those samples identified with the southern group comprised fish that were consistently larger than those identified with the northern group. In every instance where both groups were represented in the same estuary, the smaller fish occurred in samples collected late in the season, and, in most cases, there was little or no overlap in the length distributions. There is little evidence, however, that progeny from the autumn spawning contribute appreciably to the juvenile stocks in estuarine nurseries north of Long Island. Numerous attempts to collect larvae and juveniles in

Table 5.--Vertebral counts and fork lengths of juvenile Atlantic menhaden in samples from Long Island, N.Y., estuarine nurseries, 1956-57[1]

Locality and date	Fish in sample	Vertebrae						Length	
		45	46	47	48	49	Average	Range	Mean
1956:	Number	Number	Number	Number	Number	Number	Number	Mm.	Mm.
Reeves Bay									
Aug. 2.....	100	-	2	80	18	-	[2] 47.16	70- 97	78.0
Oct. 10.....	97	1	30	63	3	-	[3] 46.70	45- 67	53.9
Quantuck Creek									
Aug. 3.....	98	-	7	63	28	-	[2] 47.21	61- 85	72.4
Oct. 9.....	95	-	19	73	3	-	[3] 46.83	26- 61	41.0
Carmans River									
Aug. 3.....	100	-	2	76	22	-	[2] 47.20	85-104	84.0
Oct. 8.....	98	1	39	57	1	-	[3] 46.56	45- 56	50.0
1957:									
Skilmans Creek									
Aug. 10.....	100	-	10	74	16	-	[3] 47.06	111-127	118.6
Reeves Bay									
July 13.....	100	-	20	77	3	-	[3] 46.83	38- 63	48.3
Sept. 4.....	100	1	25	68	6	-	[3] 46.70	-	-
Sept. 4.....	59	1	20	34	3	1	[3] 46.71	37- 77	51.7
Quantuck Creek									
July 14.....	100	-	15	69	16	-	[2] 47.01	86-105	94.1
Aug. 10.....	94	1	42	48	3	-	[3] 46.56	25- 50	33.2
Sept. 4.....	100	-	53	46	1	-	[3] 46.48	74- 93	82.3
Carmans River									
Aug. 9.....	94	1	39	52	2	-	[3] 46.59	34- 68	50.4
Sept. 4.....	96	1	41	52	2	-	[3] 46.57	48- 77	59.5

[1] Vertebral counts from Sutherland (1963) appendix tables 1 and 2.
[2] Southern group.
[3] Northern group.

northern estuaries from spring to early summer 1955-59 were unsuccessful, although larvae and recently metamorphosed juveniles were found in abundance beginning in midsummer. The foregoing findings suggest that the larger juveniles in Long Island estuaries were the progeny of an autumn or winter spawning, while the smaller juveniles resulted from a spring or early summer spawning.

While information on the spatial and temporal distribution of spawning is incomplete, there is sufficient evidence to demonstrate that, south of Long Island, spawning is confined to autumn and winter. Massmann, Norcross, and Joseph (1962) reported larvae in plankton tows in ocean waters off Virginia from November to May. McHugh, Oglesby, and Pacheco (1959) found larvae abundant in Chesapeake Bay in late April and early May. Reintjes (1961) reported the occurrence of eggs and larvae along the North Carolina coast from November to March, but none during other months of the year. Higham and Nicholson (1964) reported fish in spawning condition in catches off the North Carolina coast during autumn and winter only.

Although spawning apparently takes place throughout the period that the fish occur in inshore waters north of Long Island, there are two peaks--one in spring and the other in autumn. Little spawning is indicated between June and August. Perlmutter (1939) found maximum numbers of eggs and larvae in Long Island waters in May and only scattered numbers during summer. Wheatland (1956) and Richards (1959) collected eggs and larvae

in Long Island Sound from May to October, and found greater numbers in spring and autumn. Herman (1963) obtained eggs and larvae in Narragansett Bay, R.I., from May through August and in late October, and he postulated a split spawning season in that locality, with autumn spawning being more productive. Scattergood, Trefethen, and Coffin (1951) reported that spawning fish occurred in Maine and Massachusetts waters in August and September. Higham and Nicholson (1964) found fish in spawning condition in purse seine catches north of Long Island from June to October and concluded that spawning in those waters reached a peak in October, with the suggestion of an earlier peak in May.

It seems clear, then, that two distinct groups of adults occur together from Long Island northward--one which spawns in spring, and the other in autumn. In this study, samples of spawners and nonspawners were collected simultaneously from pound net catches in Long Island and Cape Cod waters in spring, and it is known that mixed schools of spring and autumn spawners live together in these waters through summer (Higham and Nicholson, 1964). They are subject, therefore, to the same environment. If the reproductive cycle were governed primarily by environment, then it would be expected that the fish would mature and spawn at the same time, and variations in these responses would be random. Morphological differences also would be obscured. Results of the present study show, however, that irrespective of the locality in which autumn spawners were taken, their mean vertebral counts were similar. This was also true for spring spawners. But comparisons of the mean counts of autumn spawners with those of spring spawners showed significant heterogeneity.

The seasonal difference in spawning times of individuals in northern waters indicates a fundamental difference in response to the environment. Spring and autumn spawnings (and early development of young) apparently take place under entirely different temperature conditions. In figure 2 are plotted the monthly means and the daily ranges of surface water temperature for 1957-59 in localities where samples of fish used in the present study were collected. Temperatures near Cape Cod and Long Island not only were similar, but the means in April and May were from 4° to 13°C. lower than those in September and October, with overlap in ranges occurring only in May (Ambrose Lightship was off station in May each year.). Temperatures near Long Island in September and October were similar to those off North Carolina in November and December. This suggests that the southward migration of autumn spawners from Long Island to the Carolinas may be governed by their physiological response to temperature. This argument seems to be supported by the lack of significant

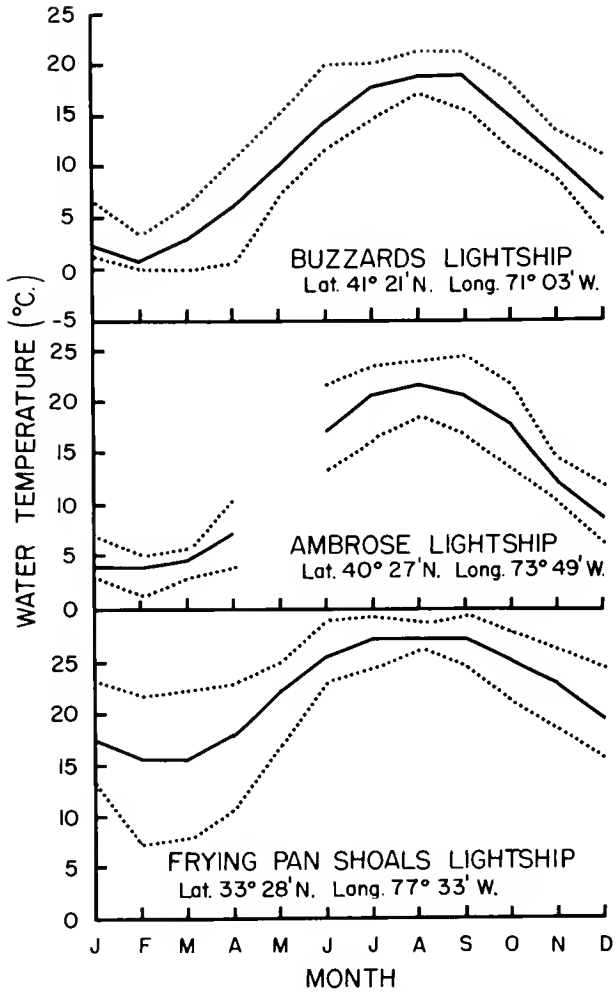

Figure 2.--Monthly range and mean temperatures at three lightship stations along the Atlantic coast of the United States, 1957-59.

variation in the meristic counts of juveniles that were presumed to have originated from the autumn spawning from Long Island southward (Sutherland, 1963).

There is evidence of other biological differences between autumn and spring spawners. For example, the mean ages and lengths of spring spawners differed from those of autumn spawners (table 1). Allowing for the advance in age that takes place between autumn and spring each year (arbitrarily on January 1), I found that both the mean age and mean length of autumn spawners off North Carolina were significantly lower than those of the spring spawners taken in Cape Cod and Long Island waters in spring. There was, however, no significant difference between autumn spawners and nonspawners taken in northern waters in spring. This suggests that autumn spawners either suffered a greater fishing mortality or were recruited at a younger age and at a shorter length than spring spawners, or both.

There also appears to be a consistent difference in the relative abundance of the two spawning groups. Higham and Nicholson (1964), for example, showed that from Long Island northward, somewhere between 12 and 18 percent of the fish in purse seine catches in October 1958, 1959, and 1960 were sexually inactive. In the present study, the proportion of spring spawners in individual samples collected in these same waters in May was between 13 and 20 percent of about the same total numbers of fish caught in each corresponding October. The relatively small numbers of nonspawners in the autumn catches and spring spawners in spring catches north of Long Island indicate that spring spawners probably constituted a much smaller group than autumn spawners.

The similarity in the vertebral counts of juveniles in northern estuaries and of spring spawners from adjacent ocean waters further emphasizes the distinctness of a northern group of fish which appears to be physiologically and genetically adapted to life under conditions of lower temperature. Thus, the inverse relation between vertebral number and temperature noted for many clupeoid fishes (Barlow, 1961) does not seem to hold for Atlantic menhaden.

In the present study, the hypothesis was that no more than two discrete groups of spawners were present simultaneously in the different localities, and the data confirm that this conclusion, in general, agrees with the known facts concerning the occurrence of spring- and autumn-spawned juveniles in estuarine nurseries and the seasonal occurrence of sexually active fish in the commercial catches. Some spawning, however, occurs in waters north of Long Island through summer (Herman, 1963). Furthermore, spawning by younger, smaller fish occurs from North Carolina southward beginning in September or October (in advance of the arrival of the larger, older spawning fish from farther northward). The relationship of these additional spawning groups should be investigated as soon as practicable since they must be considered in answering the question of population structure.

In view of the results of this study, I recommend that the meristic studies be expanded to include all known spawning groups. Other meristic and/or morphometric characters also should be included to provide estimates of the relative proportions of discrete subpopulation components in mixed samples of fish. Growth, serological, and fecundity studies also should be undertaken since these will yield ancillary information that, when combined with results of meristic studies, might lead to an understanding of the structure of the Atlantic menhaden population.

SUMMARY

1. Vertebral counts of 6,048 adult Atlantic menhaden (Brevoortia tyrannus) collected off Cape Cod, Mass., Long Island, N.Y., and Beaufort, N.C., from 1957 to 1960 were analyzed to determine if autumn (October-December) and spring (April-May) spawners were distinguishable by this meristic character.

2. Variation between sexes and within and between year classes was found to be negligible.

3. Two discrete groups of spawners--one occurring in Cape Cod and Long Island waters in spring and the other occurring in Long Island and North Carolina waters in autumn--were identified on the basis of mean vertebral count. The mean count of spring spawners was 46.914, and of autum spawners, 47.031.

4. Comparison of mean counts of spawners in three successive year classes (1955-57) with those of juveniles in the same year classes from estuarine nurseries showed that lower mean counts were associated with spring spawning north of Long Island.

5. The tendency for mean vertebral counts of reproductively isolated groups to follow a distinct pattern for several years suggests that the observed differences are genotypic in origin.

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