VARIATIONS IN SIZE AND LENGTH COMPOSITION OF ATLANTIC MENHADEN GROUPINGS

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ABSTRACT

This paper gives estimates of size (weight) and length composition of summer schools and fall school-aggregations of Atlantic menhaden based on single-set purse-seine catches and accompanying catch samples obtained in 1955-62. The data show that the fish school by length and the average size of summer schools decreases as the apparent abundance of fish in a given area of the coast decreases. The significance of the school concept in the study of the dynamics of the population and the effects of fishing upon it are discussed, and additional avenues of research are suggested.

The Atlantic menhaden, *Brevoortia tyrannus*, is a schooling fish that occurs in the western Atlantic Ocean from Nova Scotia to Florida and is the object of a purse-seine fishery over most of its range (Reintjes, 1969). The fishery is based on seasonal appearances of the fish schools in shallow waters overlying the inner half of the continental shelf (Roithmayr, 1963). Fishermen and aerial fish spotters, who locate and assist in the capture of menhaden, have a working knowledge of school size, composition, and behavior, but there exists little quantitative information on these and other aspects of the schooling phenomenon. Of primary interest to the fishery biologist are the degree to which the fish school by size, the relationship between size of schools and size of fish within schools, and the variation in size of schools in relation to changes in abundance of the fish and to fishing. These aspects of Atlantic menhaden schooling are the subject of this paper.

The nature of density and fishery-related changes in the schooling of various pelagic marine fishes is not well understood, but sufficient evidence was put forward by different workers to indicate insight into the importance of this behavioral phenomenon. The significance of the school concept in the study of the dynamics of an exploited fish population whose members are grouped and differentially distributed by size was apparently first recognized by Thompson (1926) and further elaborated by Sette (1943) for the Pacific sardine (*Sardinops sagax*). Much of the quantitative information on fish schooling dynamics has come from work on tunas. Schaefer (1948) and Brock (1954), for example, discussed some implications of observed variations in the size of fish within and between schools in the design of a sampling system for yellowfin (*Thunnus albacares*) and skipjack (*Euthynnus pelamis*) tuna stocks, respectively. Orange, Schaefer, and Larmie (1957) and Broadhead and Orange (1960) offered evidence of fishery-related changes in the schooling dynamics of yellowfin tuna, while Brock (1962) considered implications of the interrelationship between the size and number of yellowfin tuna forming a school and the success of longline fishing. June and Reintjes (1959) established that the Atlantic menhaden also schools by size, and they concluded that the school is therefore the appropriate unit for sampling the size, age, and sex composition of the population. They further demonstrated seasonal and annual variations in the estimated number and geographical distribution of purse-seine sets on menhaden schools in a series of reports beginning with 1955 (June and Reintjes, 1959), and Roithmayr (1963)

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summarized these data for the years 1955-59. There has been no further elucidation of the schooling dynamics of this fish. This study pursues that objective.

SOURCES AND TREATMENT OF DATA

The basic data consisted of fishing logbooks maintained aboard menhaden vessels for use by the National Marine Fisheries Service and reduction plant records of daily vessel landings from 1955 to 1962. Of the single-set catches recorded in the logbooks, only those for which the "hailed" catch was within 10% of the plant weights were used in the analyses. Vessel landings at the reduction plants were converted to metric tons.

I assumed that each purse-seine set during the "summer fishery" (April-September) was made on a discrete school of Atlantic menhaden. Sets made on large aggregations of fish that appeared off Long Island in late September or early October (June and Nicholson, 1964) and off North Carolina in November and December were considered separately.

Despite the rigorous screening of fishing logbooks, several sources of error may have been involved in the identification of single-school catches and estimates of school size. Foremost of these are (1) a portion of a school may have escaped during capture, (2) a variable loss in weight from decomposition may have occurred within single-school catches of the same initial size (such losses would be proportionately greater during warmer weather and in catches made at the beginning of the fishing day), and (3) a single recorded set may have actually included more than one set. Items (1) and (3) would have a greater effect on the catch estimates, but there is no way of determining the extent of these sources of error in this study; item (2) must be considered a random factor.

Catch samples, which provided measures of fish size, were taken from daily vessel landings at reduction plants along the Atlantic coast (Figure 1) as part of a routine catch-sampling program begun in 1955 (June and Reintjes, 1959). Fish lengths were grouped in ½-cm classes. The mean length, variance, and standard deviation and the mean weight, in grams, of fish in each catch sample were computed.

The number of fish within a single-set catch was determined by dividing the weight of the catch by the mean weight of the fish in the catch sample. A catch sample was obtained from 275 single-school catches during the summer fishery and from an additional 64 single-set catches from the large fall aggregations of fish off Long Island (23 sets) and North Carolina (41 sets).

Detailed logbook information and accompanying plant weights were available for 2,643 single-school summer catches and an additional 286 single-set fall catches off Long Island (138 sets) and North Carolina (248 sets). The number of single-school summer catches for which there were data constituted about 1% of an estimated 240,000 purse-seine sets made during the 8 seasons. Except for 1961 and 1962, when a combined total of only four single-school summer catches were recorded for the South Atlantic Area, single-set catches were taken throughout the range and period of fishing and are therefore believed to be representative of the schools or larger aggregations of fish into which the population was divided.

SEASONAL GROUPINGS OF THE FISH

Examination of 2,643 single-school summer catches indicated wide variation in school size (weight). A plot of the combined frequencies of single-school catches for the 8 seasons, by 3-ton size classes (upper panel, Figure 2), shows a pronounced skewness in the distribution toward smaller catches, with the mode occurring in the 4- to 6-ton size class. Single-school catches ranged from 0.3 to 103 tons. The grand mean for the 8 seasons was 16.6 tons, with a standard deviation of 12.25 tons. The size-frequency distributions of single-school catches in individual seasons (lower panels, Figure 2) also were asymmetrical and, without exception, similar in shape to that of the combined data. The maximum frequency in every year fell in either the 4- to 6-ton or the 7- to 9-ton size classes.

Although there were exceptions in some years, larger schools were generally found in the north-

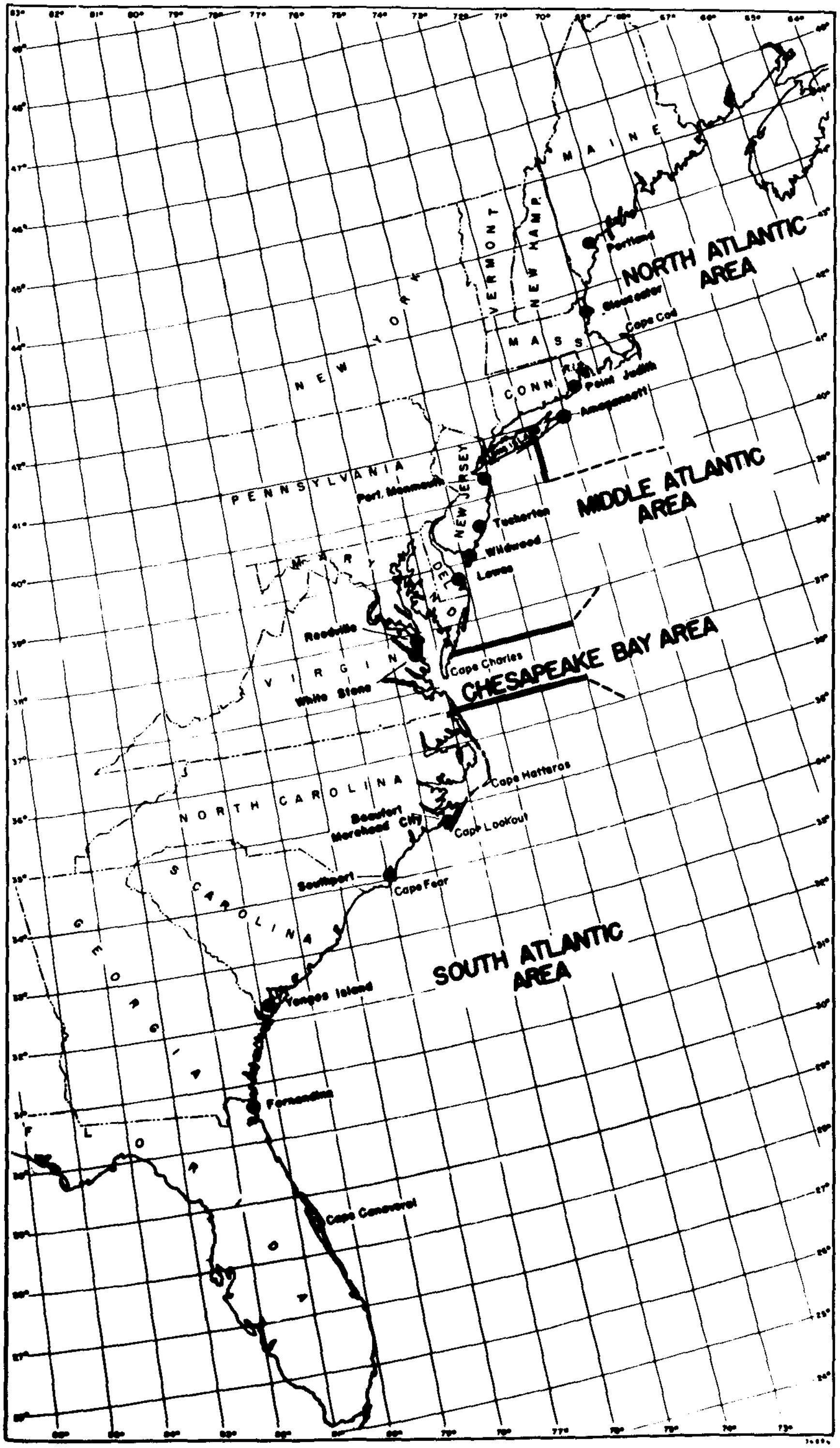

FIGURE 1.—Locations of reduction plants where Atlantic menhaden catch samples were collected and the four major geographical areas used in summarizing the biostatistical data.

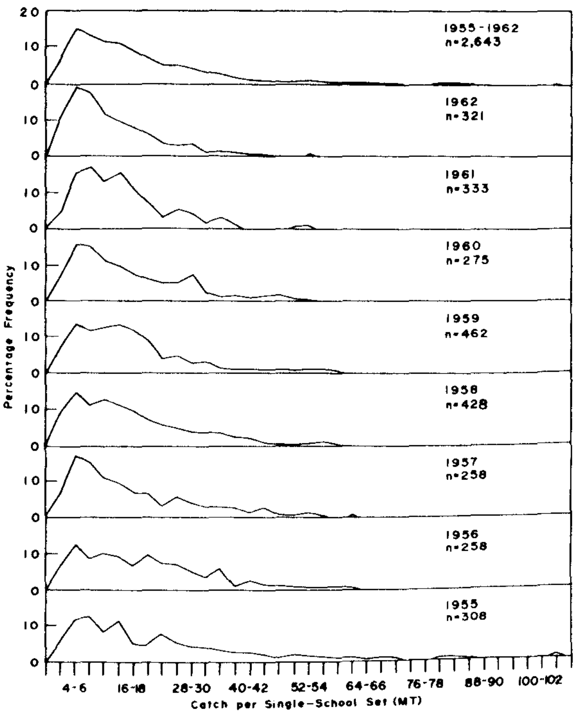

FIGURE 2.—Percentage size-frequency distributions of 2,643 single-school summer purse-seine catches of Atlantic menhaden, 1955-62.

ern part of the range during the summer, and progressively smaller schools occurred at lower latitudes. Comparison of the mean catch per single-school set within the four major areas of the summer fishery (Table 1) shows that schools in the North Atlantic Area averaged about 21 tons per set and 5 to 9 tons heavier than those in other areas. Schools in the Middle Atlantic Area were intermediate in size, averaging about 16 tons per set, while those in the Chesapeake Bay and South Atlantic Areas were smallest, averaging about 13 tons per set.

Size of summer schools declined from 1955 to 1962. The mean catch per single-school set in 1955 was 22 tons; it decreased and fluctuated around 16 tons from 1957 to 1960, and in 1962 it was only about half that in 1955 (Table 1). This decline was largely attributable to a reduction of school size in the North Atlantic and Middle Atlantic Areas, where decreases in the means amounted to about 40% over the 8-year period. In general, mean school size in the Chesapeake Bay and South Atlantic Areas fluctuated only slightly about their grand means. The high mean for Chesapeake Bay in 1955 resulted from several large single-school catches recorded at the beginning of the fishing season and probably is atypical (see also p. 704). Too few single-school catches were recorded in the South Atlantic Area in 1961 and 1962 (1 and 3, respectively) to be considered in calculation of these seasonal means. But in view of the relatively small size of single-school summer catches in previous years, additional data from this area in 1961 and 1962 would likely not have influenced the grand seasonal means.

There was a definite change in the grouping of the fish in autumn. In every year schools became noticeably reduced in number in surface waters of the Gulf of Maine in late August or early September, and during late September or early October large masses of fish, or "school aggregations,"[2] appeared off Long Island, only to disappear from these waters by mid or late

[2] To avoid confusion, the word aggregation is used in this paper in its general meaning and not as defined by Breder (1959).

TABLE 1.—Mean size of single-school summer catches of Atlantic menhaden from 2,643 purse-seine sets in the four major statistical areas, 1955-62. The number of sets used in calculating the means are given in parentheses.

Area	Year 1955	1956	1957	1958	1959	1960	1961	1962	Grand areal mean	Standard deviation
	metric tons									
North Atlantic	25.9(91)	26.4(75)	22.2(58)	18.8(78)	23.3(88)	19.2(80)	18.6(87)	15.8(48)	21.1(605)	15.32
Middle Atlantic	22.0(177)	17.3(154)	16.4(163)	16.7(258)	15.1(266)	15.4(163)	13.5(227)	13.2(163)	16.1(1,571)	11.72
Chesapeake Bay	21.9(19)	12.3(13)	11.0(19)	15.3(64)	12.4(28)	10.7(14)	12.0(19)	10.5(110)	12.8(286)	8.59
South Atlantic	11.5(21)	14.3(16)	10.3(18)	13.6(28)	12.5(80)	14.0(18)	---	---	12.6(181)	7.15
Grand seasonal mean	22.4(308)	19.5(258)	16.9(258)	16.7(428)	16.1(462)	16.2(275)	14.8(333)	12.7(321)	16.6(2,643)	12.25

October (Roithmayr, 1963; June and Nicholson, 1964; Nicholson, 1971a).

Single-set catches from fall school-aggregations, on the average, were larger than single-school summer catches. A plot, by 3-ton size classes, of 138 single-set catches made from large fall school-aggregations that appeared off Long Island shows a marked difference in the shape of the frequency polygon when compared with that of single-school summer catches in the North Atlantic Area (lower and middle panels, Figure 3). The ranges of the two distributions are nearly identical (3 to 102 metric tons for the fall school-aggregations), but the curve representing fall school-aggregations is more symmetrical and its mode considerably higher (40- to 42-ton size class) and in much closer agreement with the mean of the distribution (44.4 metric tons). Moreover, single-set catches from fall school-aggregations, on the average, were over twice as large, and the standard deviation of their frequency distribution was 1½ times greater than that of single-school summer catches in the North Atlantic Area (Table 2). Comparisons within years show the mean catch from fall school-aggregations to be from 1½ to 3½ times larger than the mean single-school summer catch in the North Atlantic Area.

Differentiation of summer schools and fall school-aggregations was also indicated by the fact that the mean single-school summer catch in the North Atlantic Area decreased over the 8-year period, whereas the mean single-set catch from the fall school-aggregations off Long Island generally increased (cf. Tables 1 and 2). Although the two seasonal catches were negatively correlated ($r = -0.228$), the coefficient has no statistical significance.

Following the disappearance of the fish from coastal waters of southern Long Island and elsewhere in October, large school-aggregations reappeared off the coast of North Carolina in November of every year. These aggregations were usually first intercepted by the fishing fleet in the vicinity of Cape Hatteras, N.C., and fished as they moved southwestward along the coast until they disappeared off Cape Fear, N.C., in December or early January (Roithmayr, 1963; Nicholson, 1971b).

Single-set catches from fall school-aggregations off North Carolina, on the average, were the largest recorded along the Atlantic coast. A plot of 248 catches (upper panel, Figure 3) shows a range of 1.5 to 180 tons. The grand mean for the 8-year period was 54.2 tons, with a standard deviation of 37.63 tons. Thus, these catches, on the average, were from three to nearly five times heavier than single-school summer

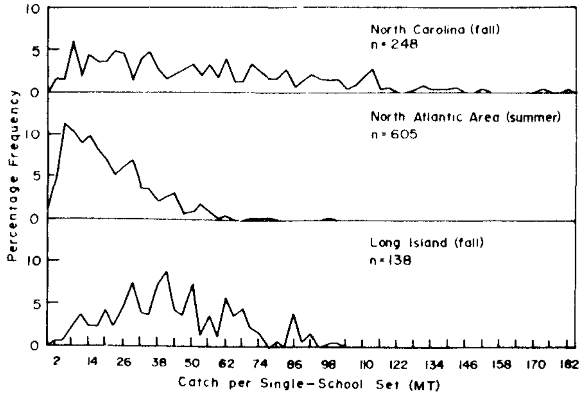

FIGURE 3.—Percentage size-frequency distributions of 138 single-set purse-seine catches of Atlantic menhaden from fall school-aggregations off Long Island (lower panel), 605 single-school summer catches in the North Atlantic Area (middle panel), and 248 single-set catches from fall school-aggregations off North Carolina (upper panel), 1955-62.

TABLE 2.—Mean size of catches of Atlantic menhaden from 138 purse-seine sets on fall school-aggregations off Long Island and 248 sets on fall school-aggregations off North Carolina, 1955-62. The number of sets used in calculating the means are given in parentheses.

Locality	Year								Grand mean	Standard deviation
	1955	1956	1957	1958	1959	1960	1961	1962		
	metric tons									
Long Island	42.3(21)	37.8(12)	39.3(16)	34.1(10)	52.2(14)	47.3(26)	39.7(18)	54.3(21)	44.4(138)	21.77
North Carolina	34.8(29)	58.0(16)	46.1(43)	44.0(22)	58.6(32)	42.2(19)	69.7(72)	57.8(15)	54.2(248)	37.63

catches in the South Atlantic Area and were most similar in size to catches made 1 to 3 months earlier from school-aggregations off Long Island (Table 2).

In summary, the data presented demonstrate heterogeneity in the seasonal and areal grouping of Atlantic menhaden. Two basic groupings are evident: (1) summer schools, which are variable in size, comprised of discrete and independent clusters of fish, and differentially distributed over the range of the species, and (2) fall school-aggregations, which are large, but of undetermined size, and found only along their apparent southward migration route.

Questions immediately arise concerning the grouping of the fish following their disappearance off North Carolina through the time of their return northward migration in early spring. During this roughly 3-month period they are usually not seen at the surface. The spring movement seems to be largely over by the time that summer schools reappear in the inshore surface waters and become available to the purse-seine fishery. Inspection of first-of-the-season single-school catches suggested that some of these were larger than those taken immediately afterward, but the numbers of such catches were too few in most years to test this hypothesis statistically. Table 3, for example, gives available data on single-school catches during the first week of fishing in each major area (cf. Table 1). A plot of school size on time, however, indicated no clear relationship and in most years was similar to that shown in Figure 4. Thus, elucidation of the off-fishing season grouping of the fish awaits further study.

LENGTH OF FISH WITHIN AND BETWEEN GROUPINGS

There was a tendency for fish within summer schools to be of similar lengths, although the difference between the largest and smallest indi-

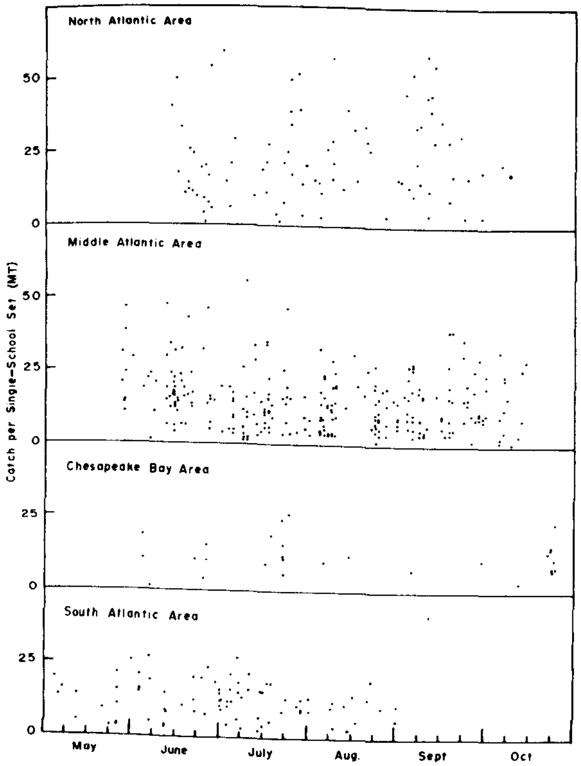

FIGURE 4.—Size of 462 single-school summer purse-seine catches of Atlantic menhaden in the four major statistical areas in 1959 plotted against time.

TABLE 3.—Size of single-school purse-seine catches of Atlantic menhaden made during the first week of the fishing season in the four major statistical areas, 1955-62.

Year	Area											
	North Atlantic			Middle Atlantic			Chesapeake Bay			South Atlantic		
	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean
		metric tons			*metric tons*			*metric tons*			*metric tons*	
1955	6	11-63	37.7	32	4-72	35.4	3	20-43	30.7	-	--	--
1956	6	7-49	29.2	12	3-47	19.6	4	4-35	17.8	-	--	--
1957	-	--	--	13	2-33	11.8	1	--	8.0	3	8-21	12.7
1958	2	12-32	21.7	3	10-23	16.0	-	--	--	-	--	--
1959	4	18-49	35.4	15	2-47	22.0	2	11-18	14.6	5	5-19	13.3
1960	3	17-41	29.4	3	10-34	23.9	-	--	--	-	--	--
1961	6	8-28	17.2	16	5-28	15.9	1	--	13.3	-	--	--
1962	3	7-30	17.5	14	7-57	23.0	3	10-29	22.8	-	--	--

viduals within a school was variable. The mean of the length range of fish within samples from 275 single-school summer catches was 5.8 cm, with a standard deviation of 2.11 cm; the range was 1.5 to 13.0 cm. The seasonal means ranged from 5.1 to 6.8 cm, with no trend indicated during the 8 years. These findings support Breder's (1959) generalization that the difference in size of fish that will form an acceptable school does not exceed 50%.

To determine if variations in the length range within summer schools were associated with the relative lengths of the members, I plotted the variance against the mean length of fish in samples from 275 single-school catches (Figure 5). The variances obviously are heterogeneous, with variation within schools being greater among fish that averaged over about 25 cm in length. A plot of variances on time failed to show any trend within or between seasons. Thus, while summer schools of Atlantic menhaden are highly length-selective, schools of mixed lengths do occur, and variation seems to be greater within schools of larger fish than within schools of smaller fish.

The length range of fish within individual summer schools was less than the length range among schools inhabiting any given area of the coast, or of the population as a whole. In Figure 6, for example, are graphed the length-frequency distributions of fish in samples from 52 single-school catches made throughout the range of the summer purse-seine fishery in 1959. The least range in length within schools was 3.0 cm and the greatest 12.0 cm; the mean difference was 6.1 cm, with a standard deviation of 2.42 cm. In general, these data show that the lengths of fish found in the different areas of the coast varied considerably, and there was a decrease in

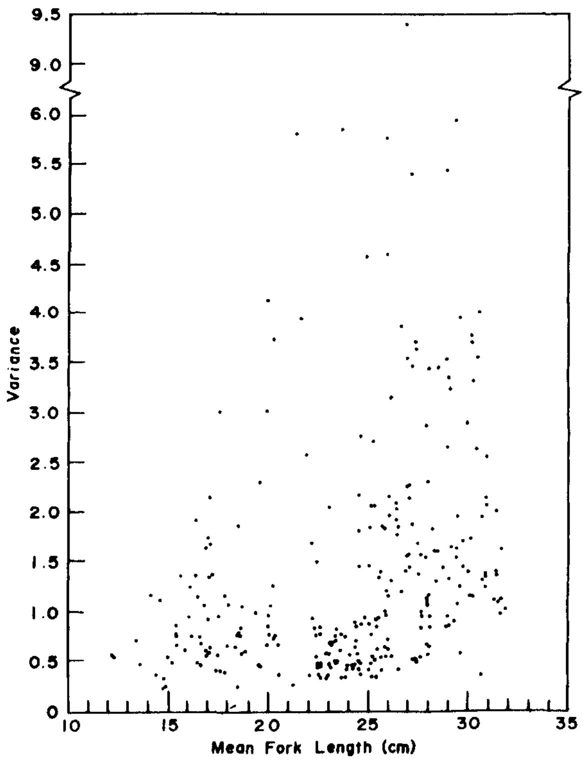

FIGURE 5.—Variance plotted against the mean of the length-frequency distribution of Atlantic menhaden in samples from 275 single-school summer purse-seine catches, 1955-62.

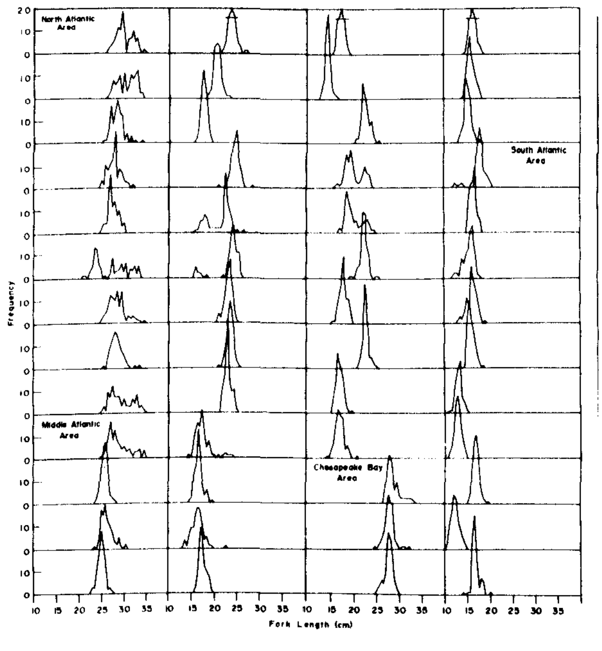

FIGURE 6.—Length-frequency distributions of Atlantic menhaden in samples from 52 single-school summer purse-seine catches in 1959. The samples are grouped by major statistical areas and arranged in order of decreasing latitude.

length with a decrease in latitude. But the important features of interest are the unimodality of most of the distributions, the decrease in variability within schools as the fish get smaller, and the comparatively narrow range of fish length within schools in contrast to the wide range of fish length within each area as a whole (cf. Nicholson and Higham, 1964). In the Middle Atlantic Area, for example, the length range within single-school catch samples varied from 3.0 to 10.1 cm, whereas the length range for the combined single-school catches sampled in that area was 21.5 cm (13.0 to 34.5 cm). So the segment of the population inhabiting any given area of the coast during the summer is evidently stratified, with each stratum comprised of discrete schools of fish grouped according to length.

Fall school-aggregations off Long Island consisted of large fish that were only represented in the North Atlantic Area during the summer. Length-frequency distributions of fish in samples from 23 single-set catches from these school-aggregations tended to be unimodal and contained relatively few fish under 25 cm (Figure 7). The range in length of fish within individual catch samples varied from 4.0 (28.0 to 32.0 cm) to 11.0 cm (23.0 to 34.0 cm). The mean length range within samples (7.3 cm, with a standard deviation of 1.81 cm) was slightly greater than that within samples from single-school summer catches in the North Atlantic Area (6.6 cm, with a standard deviation of 2.02 cm), but the difference between the means has no statistical significance.

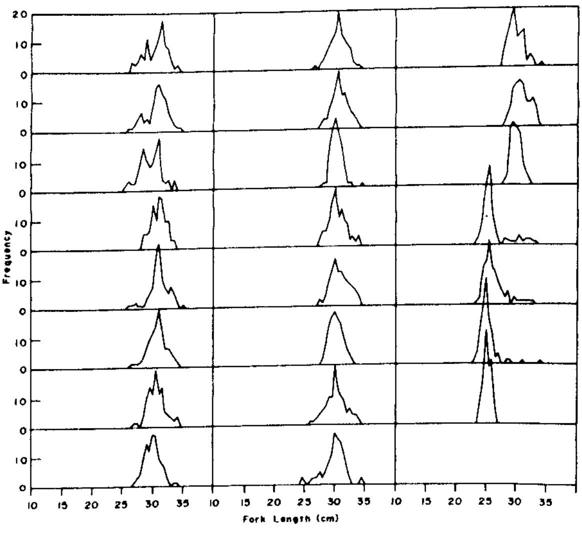

FIGURE 7.—Length-frequency distributions of Atlantic menhaden in samples from 23 single-set purse-seine catches from fall school-aggregations off Long Island, 1955-62.

The fall migratory school-aggregations off North Carolina consisted of length-groups represented farther northward during the summer, and individual aggregations contained fish of similar lengths. Fish lengths represented in samples from 41 single-set catches from these school-aggregations ranged from 8.5 to 35.0 cm (Figure 8). Because of selective fishing by the fleet on school-aggregations comprised of larger fish, the catch samples are accordingly weighted. The smallest length groups include young-of-the-year fish which had emigrated from estuarine nurseries at the end of the summer (June and Nicholson, 1964; Kroger, Dryfoos, and Huntsman, 1971). The most striking feature of the length-frequency curves is the relative homogeneity of fish lengths within individual school-aggregations, i.e., small fish are not represented in catch samples containing large fish, or vice versa. The least range in length within samples was 4.0 cm (9.0 to 13.0 cm) and the greatest 12.0 cm (22.0 to 34.0 and 22.5 to 34.5 cm). The mean of the range in length within samples was 8.4 cm, with a standard deviation of 6.13 cm. This was the largest mean difference and the greatest variation about the mean for any group of samples examined in this study. The length-frequency distributions of fish over about 25 cm were similar to those of single-school summer catches in the North Atlantic Area and to single-set catches from fall school-aggregations off Long Island (cf. Figure 7).

From an analysis of length and age data for 1955 to 1958, June and Nicholson (1964) postulated that these large school-aggregations that migrated southward along the North Carolina coast in November and December comprised portions, if not all, of the stocks which had spent the summer north of Cape Hatteras, N.C. More detailed analysis of the length-age data by Nicholson (1971a) and results of tagging studies

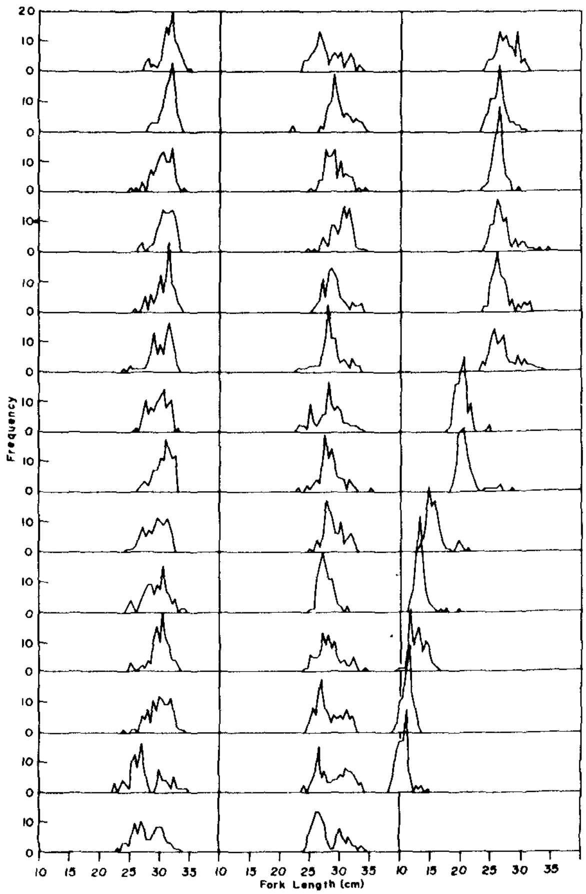

FIGURE 8.—Length-frequency distributions of Atlantic menhaden in samples from 41 single-set purse-seine catches from fall school-aggregations off North Carolina, 1955-62. *The samples are arranged in order of decreasing fish length.*

(Cheek et al., 1970) have confirmed and elaborated this hypothesis.

Briefly, the length-frequency data presented show a strong tendency for Atlantic menhaden to group by length. Summer schools are comprised of fish that are more nearly of the same length than is found among schools within any given area of the coast, or within the population as a whole, and there is an increase in the average length of fish within schools from south to north. Fall school-aggregations, which are usually fished only off Long Island and North Carolina, also consist of fish of similar lengths, but lengths within aggregations tend to be more variable than within summer schools.

SIZE OF SUMMER SCHOOLS IN RELATION TO FISH LENGTH

There was wide variation in the size (weight) of summer schools in relation to the average length of fish within a school. A plot of catch against mean length of fish in the 275 single-school catches (Figure 9) suggests a tendency for larger fish to occur in larger schools. The correlation between school size and mean fish length ($r = 0.144$) differs significantly from 0 ($P < 0.05$), and the relationship evidently is linear, since the arithmetic correlation coefficient is higher than that between log school size and log mean fish length ($r = 0.095$), or between log school size and mean fish length ($r = 0.103$). Comparison of the arithmetic correlation coefficients for the individual years, however, indicated heterogeneity ($\chi^2 = 17.14$; $P < 0.05$), so I plotted the data for each year separately and calculated trend lines (Figure 10). The occurrence of larger fish in larger schools is evident in some years, but in other years the trend was reversed, or there was no apparent relation between the two variables. Unequal representation of various length groups in different years may be responsible for the apparent heterogeneity of the data, but I conclude that annual

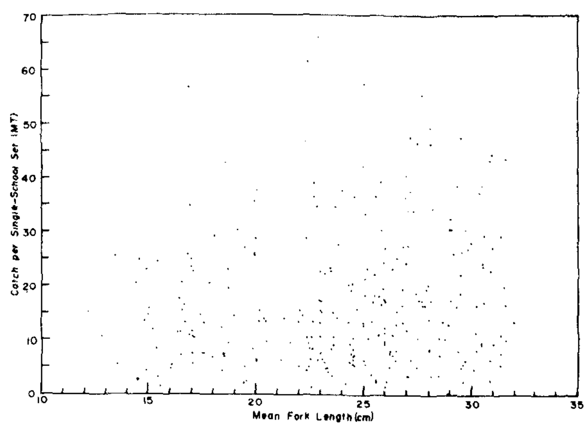

FIGURE 9.—Size of 275 single-school summer purse-seine catches of Atlantic menhaden plotted against the mean length of the fish in catch samples, 1955-62.

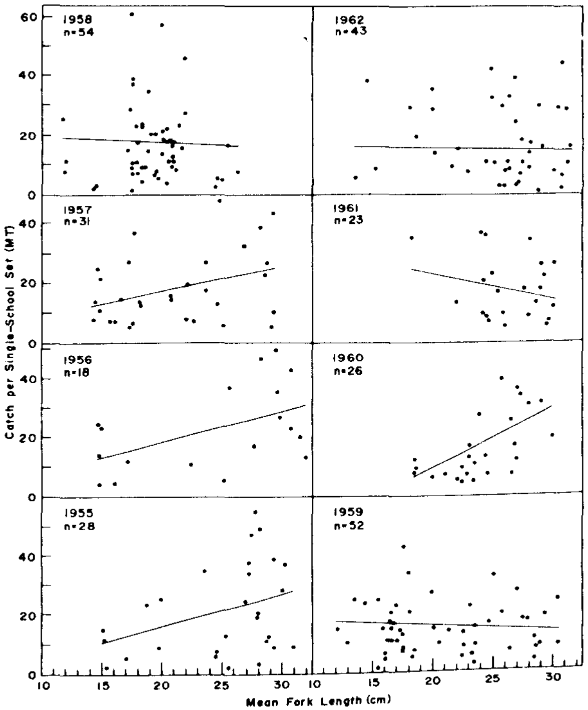

FIGURE 10.—Relationship between the size of single-school summer purse-seine catches of Atlantic menhaden and the mean length of fish in the catch sample, 1955-62.

differences in size of summer schools, which are independent of fish length, probably occur.

NUMBER OF FISH WITHIN SUMMER SCHOOLS IN RELATION TO FISH LENGTH

The number of fish within a school varied widely but, on the average, decreased as fish length increased. A plot of the estimated number of fish on the mean length of fish within the 275 single-school summer catches (Figure 11) indicates an inverse relationship between the two variables. The trend appears curvilinear; however, there is little difference among the correlation coefficients between the numbers of fish and their mean length ($r = -0.599$), between log number and mean fish length ($r = -0.597$), or between log number and log mean fish length ($r = -0.585$); all coefficients differ significantly from 0. The estimated number of fish within schools ranged from 500 (mean fish length 28.9 cm) to 655,400 (mean fish length 16.8 cm), with a mean of 86,776 fish.

In interpreting the above findings, it must be kept in mind that estimates of fish number are indirect and therefore subject to systematic bias. Furthermore, changes in the relation of school size (weight) and fish length between years were indicated in the previous section; therefore, a common regression equation may not be representative of actual changes in the numbers of fish of given size within schools. Accordingly, a trend line was not fitted to the data in Figure 11.

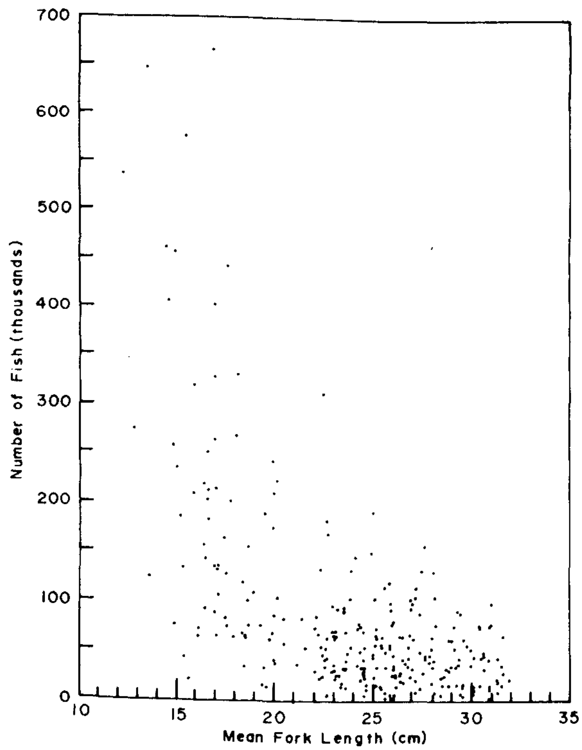

FIGURE 11.—Estimated number of Atlantic menhaden in 275 single-school summer purse-seine catches plotted against the mean length of fish in the catch sample, 1955-62.

SIZE OF SUMMER SCHOOLS IN RELATION TO APPARENT ABUNDANCE OF THE FISH

It was shown earlier that the mean single-school summer catch declined over the 8-year period in the two northern areas and fluctuated randomly in the two southern areas. To determine if these trends were an artifact of sampling or actually reflected variations in apparent abundance of the summer stock in the respective areas, I plotted the average catch per vessel week given by Nicholson (1971b) against the mean single-school summer catch in the corresponding season. There was good agreement between the two estimates in every area (Figure 12), but the relationship was closer for the South Atlantic and Middle Atlantic Areas than for the Chesapeake Bay and North Atlantic Areas. The correlation coefficient for the South Atlantic Area is significant at the 1% level and, that for the Middle Atlantic Area at the 5% level. Although the coefficients for the Chesapeake Bay and North Atlantic Areas are positive, neither differs significantly from 0. These findings indicate that summer schools became smaller as stock abundance in a given area decreased.

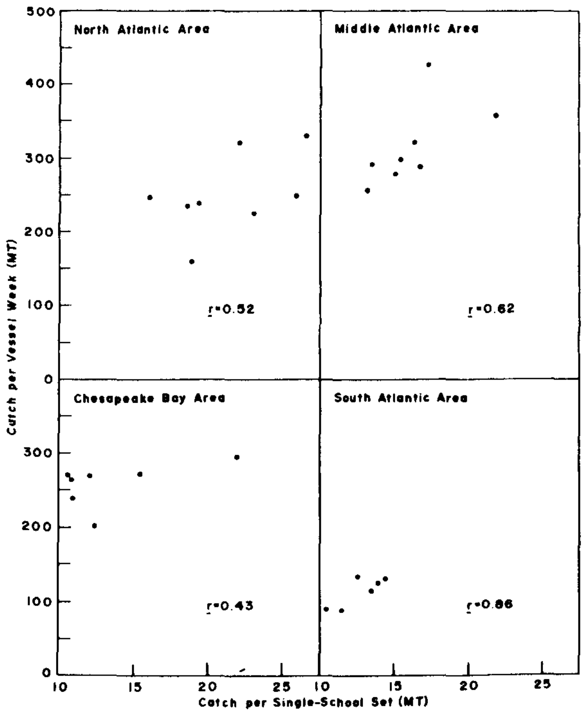

FIGURE 12.—Relationship between the purse-seine catch of Atlantic menhaden per vessel week and the mean single-school summer catch in the major statistical areas, 1955-62.

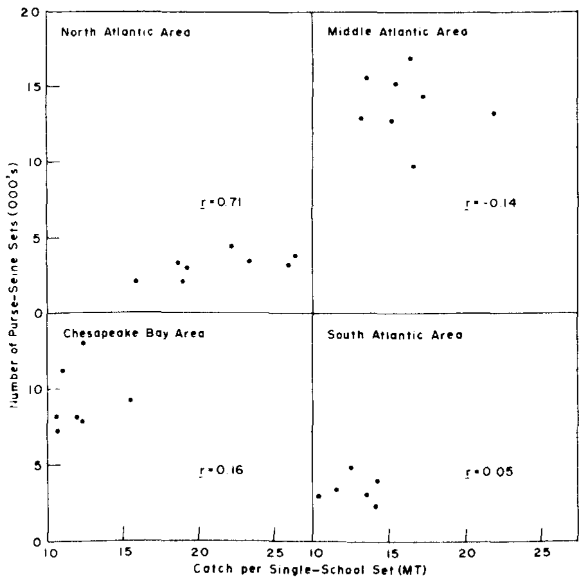

FIGURE 13.—Relationship between the estimated number of purse-seine sets for Atlantic menhaden and the mean single-school summer catch in the major statistical areas, 1955-62.

The relation between school number and school size is also of interest in assessing changes in stock abundance. A plot of the seasonal number of successful purse-seine sets (a measure of school density) given by Nicholson (1971b) on the corresponding mean single-school summer catch (Figure 13) shows a wide scattering of points within areas and considerable variability between areas. The correlation coefficient is positive for the Chesapeake Bay and North Atlantic Areas, negative for the Middle Atlantic Area, and about 0 for the South Atlantic Area, with only that for the North Atlantic Area having borderline statistical significance ($P \sim 0.05$). If these results are real, it may be inferred from the positive correlations that larger schools were associated with greater school numbers. The negative correlation, on the other hand, suggests that schools tended to be more numerous as their average size decreased.

The reasons for the apparent discrepancies in the school density-size relationship in the different areas are not clear. The lack of any trend in the South Atlantic Area may result from variable availability of the schools. Fishermen and aircraft spotters report frequent disappearances of schools from surface coastal waters early in the day and occurrences of fish inside the extensive sounds that border the summer fishing grounds in this area (this behavior pattern of the fish may be associated with tidal currents passing through the numerous inlets and their relation to the abundant plankton food supply inside the sounds). A possible explanation for the inverse relationship between school size and number in the Middle Atlantic Area is that fishing captains tend to avoid the smaller fish and smaller schools when fish are abundant. Heavy fishing in the Middle Atlantic Area may also be a contributing factor in keeping the stock broken up into smaller schools. Fishing effort in this area averaged from 1½ to 4½ times greater than in any other area and increased by about 11% over the 8-year period (Nicholson, 1971b). There very likely is some level of fishing effort that disrupts the normal schooling habits of the fish, but the interrelationships involved appear to be much more complex than can be determined from the data in hand.

The main inference to be drawn from this section is that size of summer schools is related to stock abundance in each major fishing area. The school density-stock abundance relationship, however, needs to be clarified by analysis of data collected after 1962 when the catch dropped to the lowest levels since the 1930's.

DISCUSSION

Knowledge of the nature and consistency of groupings of Atlantic menhaden is fundamental to understanding the dynamics of the population. Results of this study demonstrated that the fishable stock occurs in schools or school-aggregations during most of the year. It is also known that the young fish school from the time of their entry into estuarine nurseries as larvae (June and Chamberlin, 1959; Reintjes and Pacheco, 1966). Thus, schooling is one of the basic behavior characteristics of this fish. June and Reintjes (1959) provided initial evidence that the fish school by size and to some extent by age and also showed that schools in a given locality more closely resemble each other in composition than schools from different localities. June and Nicholson (1964) and Nicholson (1971a) described in some detail the increase in average length and age of the fish with increased latitude and inferred annual north-south movements of the fish from seasonal changes in their length and age distributions. The findings of this paper support the conclusions of the foregoing studies and provide further insight into the variability of the distribution, composition, and size of summer schools and fall school-aggregations. But one of the critical unknowns is the extent to which such variability is related to stock density and, ultimately, to fishing.

Evidence presented here indicates that the size of summer schools is a function of stock abundance. It was also shown that an inverse relationship existed between fish length and size (weight) of summer schools. These findings suggest that there probably is an optimum school size for fish of given length that is most favorable for survival. If so, there must be a level below which the population must not be fished without running the risk of disrupting schooling to the point of inflicting irreparable damage to population resilience. While these hypotheses are unprovable with present data, the inference is that schooling marine fishes that are sought by surface sightings are more vulnerable from unregulated fishing than nonschooling species that are not subject to direct observation. Slight changes in the nature and consistency of grouping of Atlantic menhaden ought therefore to be considered in assessing both short- and long-term effects of fishing on the population.

The inverse relationship shown between fish length and the number of individuals within summer schools also has important implications in regard to the yield that may be expected at different levels of fishing and to the well-being of the population. Since the fish are differentially distributed by length, with smaller fish occurring in the South Atlantic and Chesapeake Bay Areas during the greater part of the year, a disproportionate increase in the fraction of the population taken in these areas would be expected to result in a substantial reduction in the stock of larger fish available in the Middle and North Atlantic Areas. Putting it another way, a given unit of effort in the two southern areas imposes a higher fishing mortality rate. Moreover, immoderate fishing on the recruit stock in the two southern areas may also be expected to result in a drastic reduction in the size of the spawning stock. Thus, a stock-recruitment model that incorporates information on school size, number, and composition is less likely to fall short of realistic estimates of the levels of fishing commensurate with a desirable population structure and the optimum catches that may be expected therefrom.

If the role of schooling in the dynamics of the Atlantic menhaden population is to be understood, the research must be based on broader considerations than the classical methods of stock assessment. Limiting interpretation of changes in the population to simple relationships between fishing effort and catch is to ignore the dynamic aspects of fish schooling implied throughout this paper. Because of the selective nature of purse-seine fishing, fishermen's logbooks and catch records can only furnish indirect evidence of changes in the behavior and habits of the fish due to fishing. Furthermore, increased efficiency in the methods of menhaden fishing, coupled with technical improvements in fishing gear and vessels, has greatly altered long-term measures of effective fishing effort with the probable result that fishing mortality tends to be underestimated and changes in schooling of the fish minimized or perhaps obscured. Thus, there is a primary need for direct measures, independent of fishing, of school biomass and number and distribution of schools in the sea, including correlative measures of the fall school-aggregations off Long Island and North Carolina. With menhaden, direct aerial observations or photography and remote sensing are practicable (see, e.g., Roithmayr, 1970). Recent advances in underwater acoustical techniques (see, e.g., McClendon, 1968; Smith, 1970; Love, 1971) offer a supplementary means of identifying and quantitatively assessing the size and composition of menhaden schools.

Finally, development of a fully analytical approach to the role of schooling in the study of the dynamics of the Atlantic menhaden population requires a broad spectrum of information on the behavior of the fish in relation to environmental factors and other fishes. Briefly, what is needed is a more or less continuous picture of what the schools are doing. Included here are (1) the nature of short-term, i.e., day to day, changes in the behavior, structure, and distribution of summer schools in response to changes in light, salinity, temperature, currents, and food conditions, (2) the behavior of schools in isolation and in association with other fishes, (3) the primary mechanisms involved in the formation of school-aggregations and the seasonal migrations, and (4) the winter habits and whereabouts of the fish. There, for example, are no published data from which it is possible to estimate the swimming speed or endurance of which a school is capable in escaping a predator or a net. Much information can be provided from direct observations on the fish in free-swimming schools under a variety of life conditions. Aircraft are routinely employed in locating and directing fishing operations (Squire, 1961; June, 1963), yet little use has been made in menhaden research of either the information compiled by individual fish spotters or the facilities offered by the aircraft fleet. In practice this might simply require the recording of aerial observations during fishing operations and special reconnaissance flights as a means of assessing changes in the distribution and size of schools or school-aggregations during the fishing season, or mapping the migrations of this fish. Ancillary data on the behavior and physiology of the fish may be generated from experimental studies in aquaria, artificial ponds, and temporary enclosures in the sea. Any single approach to the study of schooling of Atlantic menhaden has limitations, but a combination of methods, such as those outlined here, can lead to better understanding of the obligatory nature of schooling and its role in vital life processes of individuals and dynamics of the population.

EPILOGUE

This study was planned and most of the tabulations of data and writing completed before I left the Menhaden Program in 1964, but because of the press of other duties, I was unable to fulfill an obligation to finish the work earlier. My resolve to complete it at this time was renewed when I received Dr. Reuben Lasker's letter to former associates of Dr. Elton Sette soliciting papers to be included in this dedicatory issue of the *Fishery Bulletin.*

Some of the ideas contained in this study were inspired by Dr. Sette's papers dealing with the Atlantic mackerel and the Pacific sardine and from my discussions with him of apparent similarities in the behavior and biology of the Atlantic menhaden and the Pacific sardine. It indeed is a privilege for me to acknowledge, in this place, my appreciation of Elton's influence on my concept of the disicplines of fishery biology, his sharing of an interest and enthusiasm for tropical botany and color photography, and lastly his challenging opposition on the tennis court.

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LITERATURE CITED

BREDER, C. M., JR.
1959. Studies on social groupings in fishes. Bull. Am. Mus. Nat. Hist. 117:393-482.

BROADHEAD, G. C., AND C. J. ORANGE.
1960. Species and size relationships within schools of yellowfin and skipjack tuna, as indicated by catches in the Eastern Tropical Pacific Ocean. [In English and Spanish.] Inter-Am. Trop. Tuna Comm., Bull. 4:447-492.

BROCK, V. E.
1954. Some aspects of the biology of the aku, *Katsuwonus pelamis*, in the Hawaiian Islands. Pac. Sci. 8:94-104.
1962. On the nature of the selective fishing action of longline gear. Pac. Sci. 16:3-14.

CHEEK, R. P., L. C. COSTON, R. L. KROGER, E. J. LEVI, R. O. PARKER, JR., AND G. B. SEKAVEC.
1970. Mark-recapture of Atlantic menhaden. *In* Research in fiscal year 1969 at the Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C., p. 30-34. U.S. Fish Wildl. Serv., Circ. 350.

JUNE, F. C.
1963. The menhaden fishery. *In* M. E. Stansby (editor), Industrial fishery technology, p. 146-159. Reinhold Publishing Corp., N.Y.

JUNE, F. C., AND J. L. CHAMBERLIN.
1959. The role of the estuary in the life history and biology of Atlantic menhaden. Proc. Gulf Caribb. Fish. Inst. 11th Annu. Sess., p. 41-45.

JUNE, F. C., AND W. R. NICHOLSON.
1964. Age and size composition of the menhaden catch along the Atlantic Coast of the United States, 1958, with a brief review of the commercial fishery. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 446, 40 p.

JUNE, F. C., AND J. W. REINTJES.
1959. Age and size composition of the menhaden catch along the Atlantic Coast of the United States, 1952-55, with a brief review of the commercial fishery. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 317, 65 p.

KROGER, R. L., R. L. DRYFOOS, AND G. R. HUNTSMAN.
1971. Movement of juvenile Atlantic menhaden tagged in New England waters. Chesapeake Sci. 12:114-115.

LOVE, R. H.
1971. Measurements of fish target strength: A review. Fish Bull., U.S. 69:703-715.

MCCLENDON, R. I.
1968. Detection of fish schools by sonar (eastern tropical Pacific, July-November 1967). Commer. Fish. Rev. 30(4):26-29.

NICHOLSON, W. R.
1971a. Coastal movements of Atlantic menhaden as inferred from changes in age and length distributions. Trans. Am. Fish. Soc. 100:708-716.
1971b. Changes in catch and effort in the Atlantic menhaden purse-seine fishery 1940-68. Fish. Bull., U.S. 69:765-781.

NICHOLSON, W. R., AND J. R. HIGHAM, JR.
1964. Age and size composition of the menhaden catch along the Atlantic Coast of the United States, 1959, with a brief review of the commercial fishery. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 478, 34 p.

ORANGE, C. J., M. B. SCHAEFER, AND F. M. LARMIE.
1957. Schooling habits of yellowfin tuna (*Neothunnus macropoterus*) and skipjack (*Katsuwonus*

pelamis) in the Eastern Pacific Ocean as indicated by purse seine catch records, 1946-1955. [In English and Spanish.] Inter-Am. Trop. Tuna Comm., Bull 2:81-126.

REINTJES, J. W.
1969. Synopsis of biological data on the Atlantic menhaden, *Brevoortia tyrannus*. U.S. Fish Wildl. Serv., Circ. 320, 30 p.

REINTJES, J. W., AND A. L. PACHECO.
1966. The relation of menhaden to estuaries. *In* R. F. Smith, A. H. Swartz, and W. H. Massmann (editors), A symposium on estuarine fisheries, p. 50-58. Am. Fish. Soc., Spec. Publ. 3.

ROITHMAYR, C. M.
1963. Distribution of fishing by purse seine vessels for Atlantic menhaden, 1955-59. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 434, 22 p.
1970. Airborne low-light sensor detects luminescing fish schools at night. Commer. Fish. Rev. 32(12):42-51.

SCHAEFER, M. B.
1948. Size composition of catches of yellowfin tuna (*Neothunnus macropterus*) from Central America, and their significance in the determination of growth, age, and schooling habits. *In* M. B. Schaefer and J. C. Marr, Contributions to the biology of the Pacific tunas, p. 197-200. U.S. Fish Wildl. Serv., Fish. Bull., vol. 51.

SETTE, O. E.
1943. Studies on the Pacific pilchard or sardine (*Sardinops caerulea*). I. - Structure of a research program to determine how fishing affects the resource. U.S. Fish Wildl. Serv., Spec. Sci. Rep. 19, 27 p.

SMITH, P. E.
1970. The horizontal dimensions and abundance of fish schools in the upper mixed layer as measured by sonar. *In* G. B. Farquhar (editor), Proceedings of an International Symposium on Biological Sound Scattering in the Ocean, March 31-April 2, 1970, p. 563-591. Maury Center Ocean Sci. Rep. 005.

SQUIRE, J. L., JR.
1961. Aerial fish spotting in the United States commercial fisheries. Commer. Fish. Rev. 23(12):1-7.

THOMPSON, W. F.
1926. Errors in method of sampling used in the study of the California sardine. *In* The California sardine, p. 159-189. Calif. Fish Game Comm., Fish Bull. 11.