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DETERMINING AGE OF ATLANTIC MENHADEN FROM THEIR SCALES

BY FRED C. JUNE AND CHARLES M. ROITHMAYR



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ABSTRACT

Scales of Atlantic menhaden, Brevoortia tyrannus, are described and results of detailed examination summarized for the purpose of determining whether certain recognizable rings are reliable age marks. Based on the occurrence of one or more dominant modes in monthly frequency distributions of scale measurements of two separate ring classes, it was shown that (1) the modes representing each ring remained homologous, (2) an increase in the number of rings was accompanied by an increase in the length of the scales, (3) the distance between modes representing the last submarginal ring and the edge of the scale decreased with the addition of each new ring, (4) new scale growth was greatest during the warm months of the year, reaching a maximum in the fall, and (5) scale rings are formed only once each year and thus are reliable age marks. Differences were observed in the growth of scales from fish assigned to two different ring classes, and new scale growth was found to be greatest in southern coastal waters and in younger fish. Examination of scales from fish confined over a 14-month period showed that only one ring had formed, thus verifying the validity of the scale method.

IV

DETERMINING AGE OF ATLANTIC MENHADEN FROM THEIR SCALES

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Knowledge of the age of Atlantic menhaden, Brevoortia tyrannus (Latrobe), is useful in solving basic life-history problems of the species and is essential to an understanding of the population dynamics of the fishery. It would be difficult, indeed, to determine the number and size of year classes in the fishable stock and to compute such vital statistics as growth rate or fishing and mortality rates without a knowledge of age. In the study of these matters, being conducted by the U.S. Fish and Wildlife Service, it is of paramount importance, therefore, that some reliable method of assessing the age of individual fish be established.

Rush (1952) examined the scales of 34 Atlantic menhaden collected at Beaufort, N. C., and calculated the lengths of the fish at the time of annulus formation from scale measurements. He concluded that the observed annulus groups, when plotted against fork length, produced a normal growth curve. Westman and Nigrelli (1955) identified the ages of specimens collected in northern New Jersey and southern Long Island waters from scales, but did not establish the validity of the readings. McHugh, Oglesby, and Pacheco (1959) demonstrated that annuli in young menhaden are formed in spring and found close correspondence in ages determined from length-frequency distributions and from scales. These efforts represent the only previous records of attempts to assess the age of this species from scales. It is the primary purpose of this paper to examine these structures in some detail to determine whether certain recognizable rings are reliable age marks.

The material on which this report was based was collected by many temporary field assistants employed by the Menhaden Investigations. Drs. J. Lawrence McHugh and George A. Rounsefell critically read the manuscript.

COLLECTION AND TREATMENT OF SCALE SAMPLES

The bulk of the scales for study was obtained from samples of purse-seine landings at various ports along the middle Atlantic coast of the United States from 1952 through 1956. Data for 1952 and 1953 came from weekly or semiweekly samples of the catches landed at Lewes, Del., and Wildwood, N. J. In 1954, additional samples were obtained daily at Amagansett, N. Y., commencing in August, and periodically throughout the season at Port Monmouth, N. J. In 1955, samples for the most part were collected each day that purse-seine landings were made at Portland, Maine; Gloucester, Mass.; Amagansett, N. Y.; Port Monmouth, N. J.; Lewes, Del.; Reedville, Va.; Beaufort and Southport, N. C.; Yonges Island, S. C.; and Fernandina Beach, Fla. However, only a part of this great mass of data was used in the study. Scale collections also were obtained outside the regular purseseine fishing season from pound-, fyke-, and gill-net fisheries operating along the middle Atlantic coast and in Chesapeake Bay. Additional material included periodic collections of scales from young-of-the-year fish inhabiting estuarine nursery grounds in Indian River, Delaware. Scales also were taken from fish reared over a period of 14 months in outdoor ponds at Beaufort, N. C. Results of readings of 13,510 scale samples are reported in this study.

The procedure used in sampling the purseseine, pound-, fyke-, and gill-net fisheries involved taking random samples, each of 100 fish, from a single day's catch. The fork lengths of the fish in each sample were measured on a board having a nose block at one end and a millimeter scale inlaid along the center. Scale samples were taken from every fifth fish. Those fish from which scales were taken were weighed and the sex and stage of sexual maturity noted. Approximately 25 scales were removed from the

Note.—Approved for publication, May 21, 1959. Fishery Bulletin 171.

middle of the left side below the insertion of the dorsal fin (see p. 325). If scales were missing from this region, they were taken from the same location on the right side of the body; or if scales were missing from both sides, another fish of the same half-centimeter size class was substituted. Individual scale samples were placed temporarily in a 2-dram vial containing water and three or four drops of 2-percent phenol.

Scales were cleaned of integument and chromatophores by rubbing between the fingers and were mounted dry between two glass slides held together at the ends with cellulose tape. Usually six scales were mounted from each fish. Each scale sample was identified by a serial number, the only information placed on the slide. A few of the scale samples were placed in scale books at the time of collection and subsequently soaked and cleaned prior to mounting.

An Eberbach projector was used for viewing the scales at a magnification of $40 \times$. All scales were read by the authors, each reading the samples independently. One scale from each sample was selected for measurement. The scale chosen was free from defects and represented the most symmetrical scale in the sample. The distances from the proximate center of the base of the sculptured field (overlay fig. 1) to each

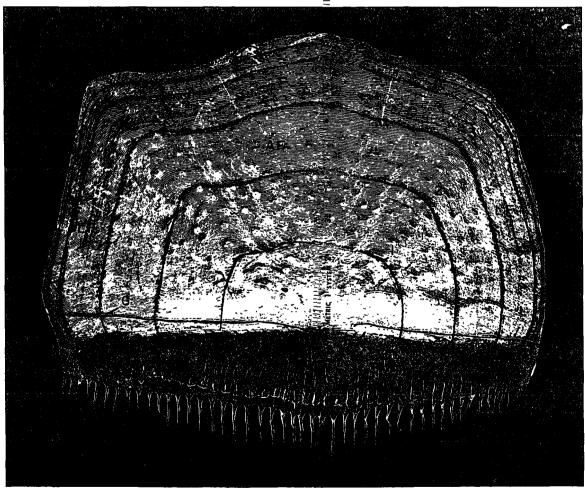


FIGURE 1.—Scale of Atlantic menhaden with five rings. AF, anterior field : PF, posterior field : LF, lateral field : SM, scale margin : G, groove ; P, pectinations ; R, ridges. Arabic numerals indicate age rings.

UNITED STATES DEPARTMENT OF THE INTERIOR FISH AND WILDLIFE SERVICE

FISHERY BULLETIN 171 (Fishery Bulletin of the Fish and Wildlife Service, vol. 60, p. 324)

CORRECTION

In figure 1, on page 324, the tracing that identifies the parts of the scale was printed directly upon the picture instead of on a separate tissue overlay. Please insert this correctly printed picture with its tissue overlay on page 324.

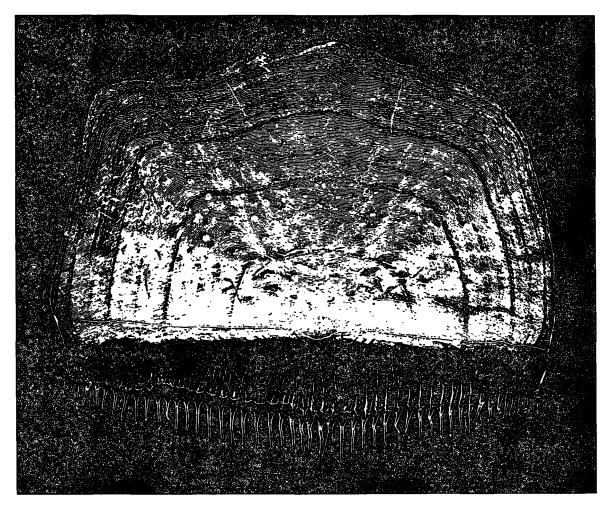


FIGURE 1.-Scale of Atlantic menhaden with five rings. See overlay for identification of parts.

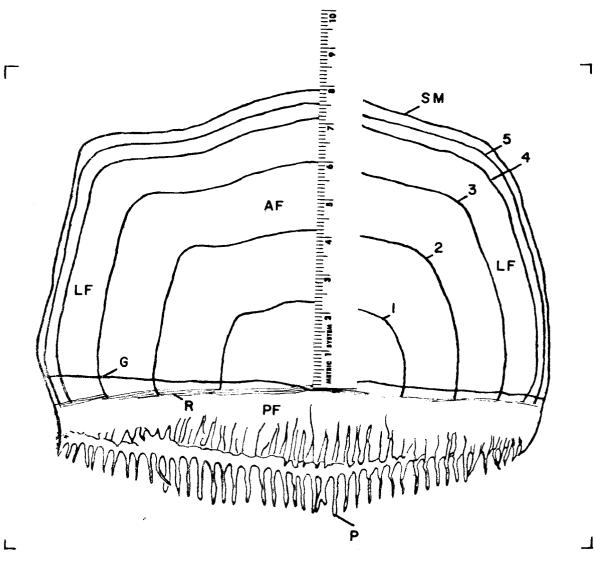


FIGURE 1-Overlay. AF, anterior field; PF, posterior field; LF, lateral field; SM, scale margin; G, groove; P, pectinations; R, ridges. Arabic numerals indicate age rings.

ring and to the margin of the scale were measured to the nearest millimeter. Measurements were marked on a Keysort card having a ruled metric scale along one edge. The independent age readings and measurements were compared and differences either reconciled or the scale samples of questionable age discarded.

DESCRIPTION OF SCALES

Scale structure in the genus *Brevoortia* indicates a specialization in development, divergent from that of most other members of the herring family. The posterior margin of the scale in young fish is serrate, in adults pectinate, and nearly vertical, whereas in most herrings the posterior margins are smooth and rounded.

In general, scales of Atlantic menhaden are adherent, translucent, and rather thin. The exposed, posterior field is granular and much deeper than long. Basal portions of the serrations or pectinations are clearly evident in this field and constitute an argument for the continual growth of the scale. The imbedded, anterior field is sculptured with ridges which run more or less parallel to the anterior margin of the scale. Usually one or more grooves cross the anterior field near and parallel to its base. In older fish, radial fissures frequently transect the anterior margin of the scale. A small, clear, somewhat semicircular area occurs at the proximate center of the base of the anterior field (fig. 1).

To determine whether differences. existed among scales from various regions of the body, scale patterns of 15 fish of varying size were examined in detail. Results showed that the largest and most symmetrical scales occurred in a median, lateral band between the tip of the flexed pectoral fin and the insertion of the dorsal fin. Furthermore, rings on the scales from this region were most clearly marked. Accordingly, all scale samples were taken from this area of the body.

EARLY SCALE GROWTH

Atlantic menhaden scales begin as cycloid scales (fig. 2). Examination of stained larval and postlarval specimens collected in the vicinity of Beaufort, N. C., and in Indian River, Delaware, during the winter and spring months of

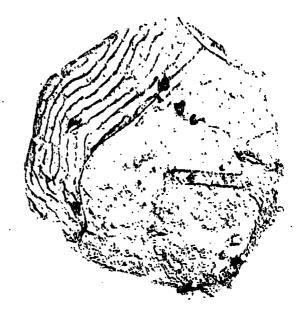


FIGURE 2.—Photomicrograph of a scale from a postlarval Atlantic menhaden.

1955 and 1956 indicated that scale formation commenced at body lengths between 24 and 30 millimeters. Detailed study of the developmental stages of larvae captured in January 1955, and reared through metamorphosis in ponds at the U.S. Fishery Laboratory at Beaufort, substantiated these findings.

Scales were first observed in the region of the caudal peduncle and along a median, lateral line on the body. Later they appeared near the base of the pectoral fins and along the posterior margin of the opercle. Appearance of the scales marks the first apparent feature of metamorphosis from larva to juvenile. In all specimens examined, the scales were fully formed at body lengths between 30 and 43 millimeters.

Growth of the scales prior to ring formation was determined from young-of-the-year fish obtained during the late spring and summer of 1956 in Indian River, Delaware. Measurements of their scale lengths are shown as percentage frequency distributions in figure 3. The first individuals from which scales could be secured were taken on May 22. The mode of the scale lengths of this group was 13 millimeters (at a magnification of $40 \times$). Growth of the scales was traced until mid-September, when the mode had progressed to 78 millimeters. All of these scales were devoid of any markings that might be interpreted as age rings (fig. 4), hence, the latter must be formed sometime after the first summer of life. Examination of many thousands of juveniles collected in other estuarine nursery areas along the Atlantic coast during the summer months of 1955 and 1956 supports this conclusion.

DEFINITION OF AN AGE RING

Recognition of age rings on Atlantic menhaden scales was based on recurrent interruptions of the uniformly spaced ridges in the anterior field. Such areas of discontinuous and irregular ridges form narrow, continuous, light bands which normally stand out in sharp contrast to the bold, continuous, and regular ridges on either side. Occasionally, such a band may

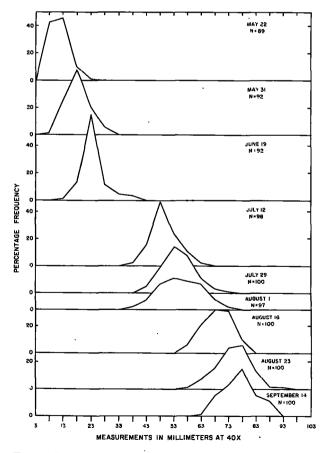


FIGURE 3.—Frequency distributions of scale-length measurements of juvenile Atlantic menhaden collected in Indian River, Delaware, in 1956.



FIGURE 4.-Scale of Atlautic menhaden with no rings.

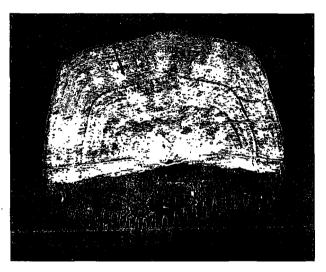


FIGURE 5.—Scale of Atlantic menhaden with one ring.

appear as a sharp line separating ridges of different elevations. These bands are separated from each other and are present in the same relative position on the scales of an individual fish. They are roughly parallel to the margin and may be traced around the entire sculptured portion of the scale. Such a band is here defined as an age ring.

Other scale features provide additional criteria for recognition of an age ring. Under magnification, the first ring usually stands out in bold relief on the posterior field, and by careful focusing, traces of additional rings may be apparent; continuations of the rings may sometimes be seen in the posterior field. Erosion of the scale at or near a ring further enhances the character of a ring (figs. 5-9).

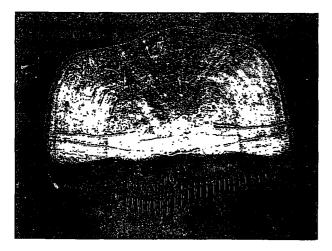


FIGURE 6.—Scale of Atlantic menhaden with two rings. The second ring is located just inside the margin.

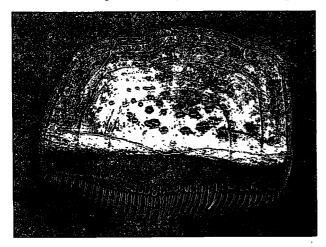


FIGURE 7.-Scale of Atlantic menhaden with three rings.

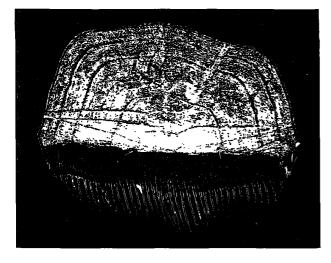


FIGURE 8.—Scale of Atlantic menhaden with four rings. 529219 0—60—2

IRREGULARITIES IN SCALE STRUCTURE

Several major irregularities in scale structure occasionally occur, and these may have affected the accuracy of some of the age determinations. Most important of these is the occurrence of accessory rings, which oftentimes resemble the defined age ring, but differ in their scarlike appearance. Such rings usually are incomplete, irregular in outline, and not parallel to the margin. Accessory rings frequently appear as folds in the sculptured pattern, and the ridges crossing such folds show a continuity and regularity, rather than the discontinuity and irregularities of the defined age ring. Furthermore, they usually occur at irregular intervals between regularly spaced and clearly marked age rings (fig. 10). Finally, and most important, accessory rings rarely are present on all scales of an individual fish.

Perhaps the most common irregularity in Atlantic menhaden scales occurs in the central area of the anterior field where the distinct, regularly spaced ridges are replaced with short, discontinuous scars. Such areas generally are granular in appearance, irregular in outline, and highly variable in relative size (fig. 11). Scales with such areas were considered to be regenerated and were not used in the age determinations.

Occasionally, there appears to be a smaller scale set off center in a larger scale. The axes of the two scales are at different angles. This condition is presumed to be the result of a younger scale being dislocated and rotated slightly in the scale pocket, since subsequent scale growth is normal and along the proper axis (fig. 12).

Additional minor irregularities in structure frequently occur in scales of older fish. These include excessive erosion of the scale at or near the location of an age ring (fig. 13); scars which are granular in appearance and devoid of ridges; small, clear areas in the sculptured portion; coarse, radial fissures in the anterior field (fig. 14); and rough, granular ridges in the central region of the anterior field. These minor defects, for the most part, do not cause any difficulty in determining the location of an age ring and normally do not occur on all scales of an individual.

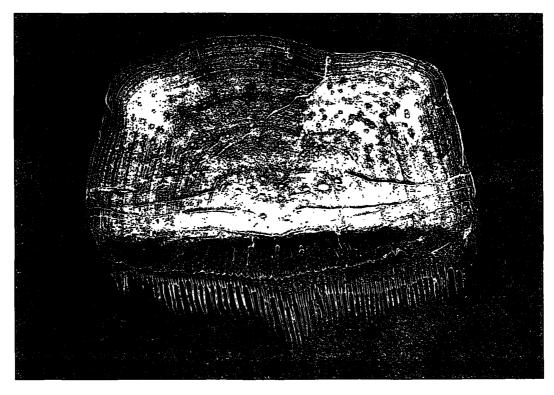


FIGURE 9.—Scale of Atlantic menhaden with 10 rings.

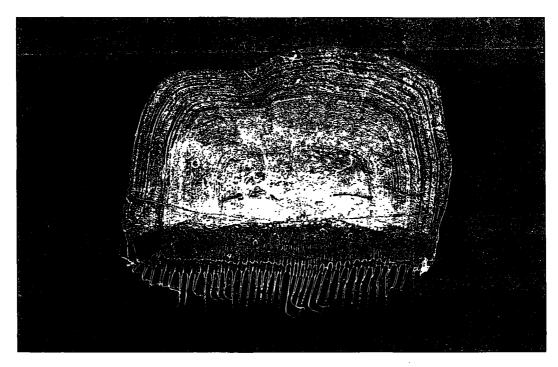


FIGURE 10.-Scale of Atlantic menhaden with three age rings and several accessory, or false, rings.

DETERMINING AGE OF ATLANTIC MENHADEN FROM SCALES

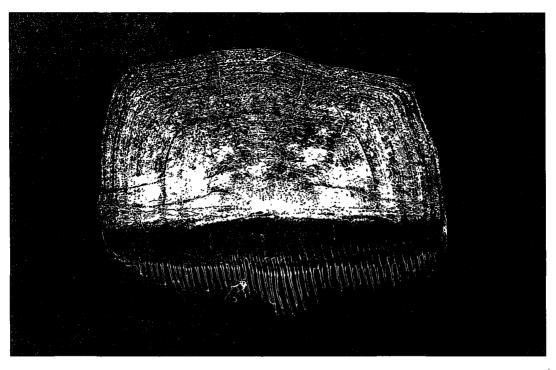


FIGURE 11.—Scale showing a regenerated central area.

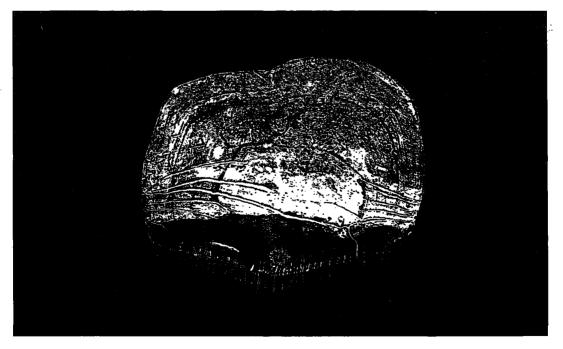


FIGURE 12.—Scale showing a rotated central area.

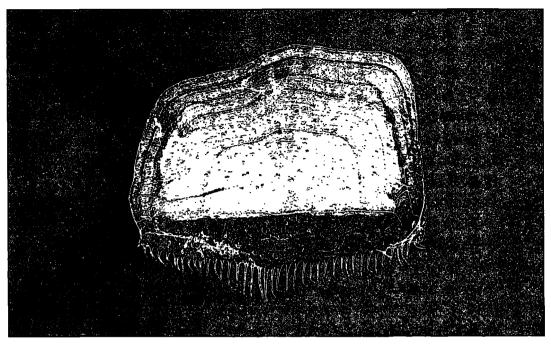


FIGURE 13.—Scale showing erosion at the location of an age ring.

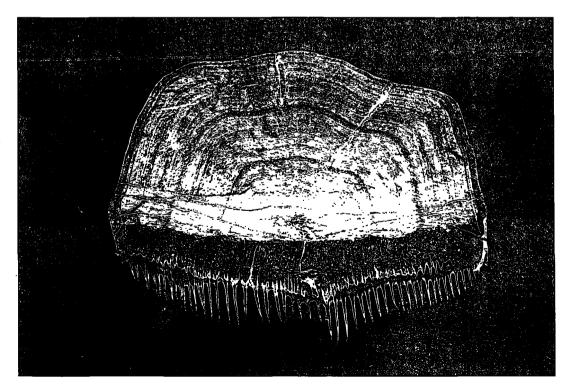
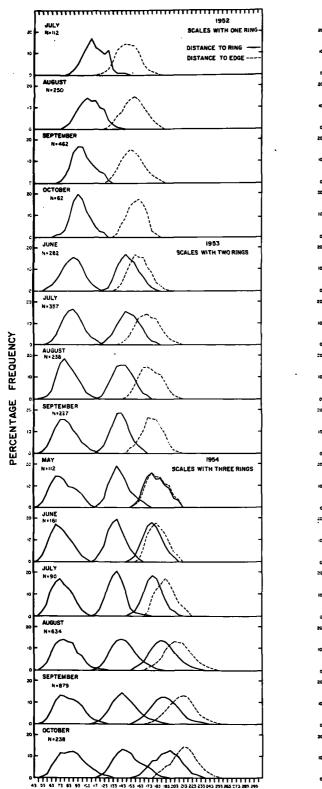


FIGURE 14.—Scale showing radial fissures in the anterior field.



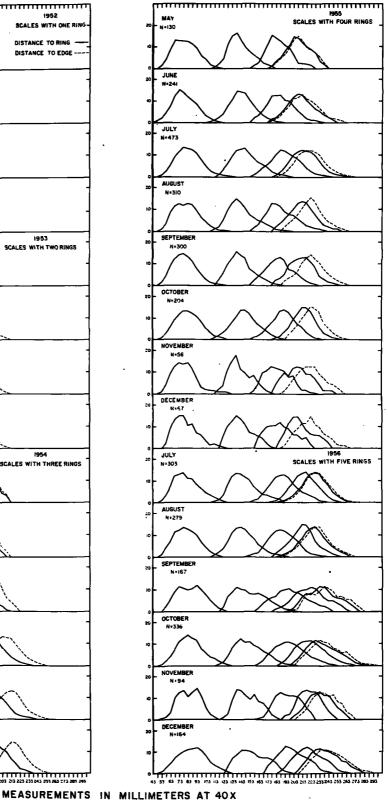


FIGURE 15.—Monthly frequency distributions of measurements of scale lengths to each ring and to the edge of the scale, 1951 ring class.

VALIDITY OF RINGS AS AGE INDICATORS

SCALE GROWTH

Evidence bearing on the validity of the scale method for determining the age of Atlantic menhaden is furnished by scale measurements, which were used to trace scale growth over a period of years. One method of establishing the validity of scale readings involves the reconstruction of the past growth history, based on either a real or assumed relation between body length and scale dimensions (Van Oosten 1929; Whitney and Carlander, 1956). In this study, however, we have used only the scale measurements. Our method yields the same results, but in terms of scale length rather than fish length. Scales arbitrarily assigned to ring-classes 1951 and 1952 were used for this purpose. Those which showed 1 ring in 1952 were designated as the 1951 ring class and those with 2 rings in 1954 were designated as the 1952 ring class. Growth of scales assigned to the 1951 ring class was followed over a period of 5 years (1952 through 1956) and of the 1952 ring class, over a period of 2 years (1954 and 1955).

Measurements of scales of the 1951 ring class which showed from 1 through 5 rings in successive years were plotted in 5-millimeter size classes as monthly frequency distributions, commencing with July 1952 (fig. 15). Absence of a commercial fishery during the winter months precluded adequate data during this period, hence, months represented by fewer than 50 fish were excluded.

Examination of figure 15 reveals several striking features in the curves, both within and between years. Most outstanding is the occurrence of one or more dominant, homologous modes in all of the monthly frequency distributions. Secondly, with the appearance of each additional ring on the scales, the mode of its frequency distribution is seen to persist in all subsequent months. However, there is an increase in the amount of overlap of the frequency curves representing each additional ring. Thirdly, the curves show an increase in the length of the scales with the addition of each new ring. Fourthly, the distance between the last two modes decreases in each successive year, and the distance from the last ring to the margin of the scale (dashed line) diminishes from year to year as each additional ring appears on the scales. Fifthly, in each year the distance from the last submarginal ring to the edge of the scale increases through the summer months, reaching a maximum width in the fall. Finally, with the appearance of each new ring, the mode of its frequency distribution is seen to be homologous with that of the marginal increments in the latter months of the previous year, indicating that a new ring is laid down on the scale sometime between late winter and late spring.

Comparison of the combined monthly samples representing each ring group in successive years for the 5-year period (1952-56) is made in figure 16. Except for the first ring, the curves show a remarkably consistent pattern with respect to the location of each ring from year to year.

Scales assigned to the 1952 ring class first appeared in numbers in our samples as 2-ring scales in 1954. A plot of their measurements, as 2- and 3-ring scales in 1954 and 1955, respectively, is shown in figure 17. The curves show essentially the same features, both within and between years, as previously described for the 1951 ring class. In general, the modes of the frequency distributions representing the first and

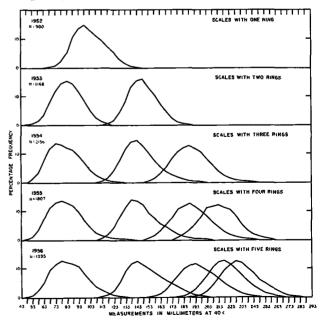


FIGURE 16.—Combined monthly frequency distributions of measurements of scale lengths to each ring, 1951 ring class.

second rings persist throughout; with the addition of the third ring, the mode of its frequency distribution persists thereafter; there is an increase in the length of the scales, both between months and between years; and the width of the submarginal zone increases during the summer in both years. The combined monthly data representing the 1952 ring class in each year (1954– 55) are shown in figure 18. Again, the curves show a fairly consistent pattern between years in the location of the first two rings.

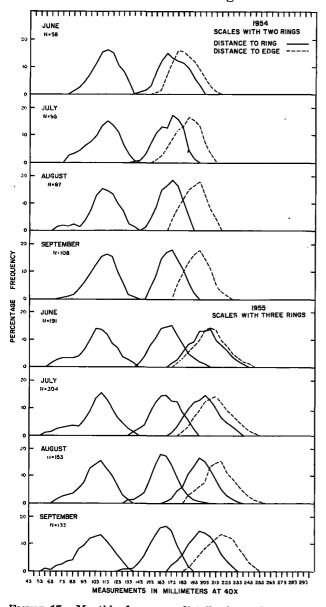


FIGURE 17.—Monthly frequency distributions of measurements of scale lengths to each ring and to the edge of the scale, 1952 ring class.

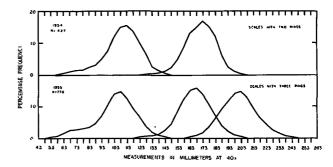


FIGURE 18.—Combined monthly frequency distributions of measurements of scale lengths to each ring, 1952 ring class.

DISCREPANCIES IN FREQUENCY CURVES OF SCALE GROWTH

While the foregoing discussion describes the general features of the frequency curves for each ring class, it is obvious that slight irregularities and discrepancies occur, both within and between each ring class. Chief among them is the failure within a ring class of homologous modes to occur in exactly the same position each month. This is particularly evident in the distance to the first ring. Frequencies of scale measurements to the first ring in the 1951 ring class (fig. 15) show a dominant mode at 108 millimeters in July which recedes to 93 millimeters in September and October. Comparison of the monthly means (table 1) indicated that these scales could not have been drawn from a homogeneous population as determined from measurements of the distance to the first ring (F = 7.86;P 0.01 = ca. 3.80). A further apparent decrease in the first year's scale growth may be seen in 1953 when the dominant mode receded from 88 millimeters in June to 78 millimeters in August and September. In subsequent years it shifted slightly in certain months, but remained relatively stable at about 73 millimeters. Furthermore, in 1953, when two rings were present on the scales, the mode of the frequency distributions representing the distance to the second ring appeared at 148 millimeters in June and July; however, by September it receded to 143 millimeters and thereafter continued to vary between 138 and 143 millimeters. Some variability also was evident in the frequency curves in subsequent years.

TABLE 1.—Frequencies	of scale	lengths (a	it 40	\times) to the
first ring of 1-ring fish	sampled	at Lewes,	Del.,	and Wild-
wood, N.J., 1952				

October	September	August	July	Size class	
	2			mm 61–65	
	2		1	66-70	
2	1	. 1		1-75	
	13 36	2		76–80	
12	30 57	13		6-90	
16	108	27)1-95	
9	69	35	11	06-100	
7	56	34		01-105	
53	41 33	41 23		106-110 111-115	
0 1	23	20 35		16-120	
i	17	16		21-125	
2	1	10		26-130	
	3	4		131-135	
		2		36-140 41-145	
				46-150	
			l ì	51-155	
62	462	250	112	Total	
96, 7	98.3	106, 9	112.4	Mean	

A slight downward shift in the location of the modes representing the first and second year's scale growth of the 1952 ring class also is evident over the period represented (fig. 17). In most months there is also a suggestion of a secondary mode at approximately 83 millimeters in the first year's scale growth.

Comparison of the modes representing the combined monthly samples for each ring class (figs. 16 and 18) shows that scales of the 1952 ring class exhibited a faster growth rate than those assigned to ring-class 1951. As 2-ring scales in 1954, the dominant mode of the first year's scale growth of the 1952 ring class is located at 113 millimeters and that of the second year's growth at roughly 173 millimeters. In contrast, the mode of the first year's scale growth for the 1951 ring class (of comparable age in 1952) is located at 83 millimeters and that of the second at 148 millimeters. Comparative growth of these two ring classes, as 3-ring scales, is demonstrated graphically in figure 19. Except for the slower growth exhibited by the 1951 ring class (solid line), the two curves are almost identical. These findings lend further confidence to the accuracy of our scale readings, for in addition to the number of rings present on the scales, those assigned to a given ring class exhibited a persistent growth pattern which distinguished them from an adjacent ring class.

Some of the discrepancies noted in the frequency curves may be attributable to the small numbers of fish represented in certain months.

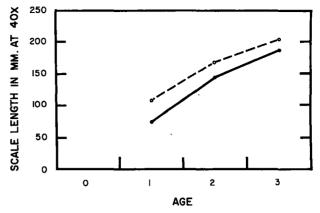


FIGURE 19.—Comparative growth rates of the 1951 (solid line) and 1952 (dashed line) ring classes as 3-ring scales.

A further source of bias lies in the fact that the bulk of our data were from fish selectively caught by purse seines. Hence, the observed progress of scale growth in successive months, and in successive years, may not have represented that of the population at large. Furthermore, comparisons between certain months were based on fish caught by purse seines and those taken by other gear and, therefore, may not have represented similar groups of fish.

Aside from these considerations, the variability in the position of homologous modes between months within each ring class is believed to be due largely to the movement of fish through a given locality during the fishing season. Based on the results of our coastwise sampling of the purse-seine catches over the past 3 years (1955 through 1957), the size of fish caught in a given locality, in general, was found to remain relatively constant or even to decrease throughout the summer; and the fish which contributed to the late summer fishery often were younger than those comprising the early summer fishery. Furthermore, fish of the same age caught in a given locality, in general, were found to be progressively smaller as the season advanced. An example is afforded from the summer catches landed at Beaufort, N.C., in 1955 (fig. 20). These findings would obtain only if the larger and older fish either were subject to a higher mortality rate, or emigrated and were continually being replaced by smaller and younger recruits. Before 1955 our sampling did not cover the range of any age group in the fishery and samples taken at the

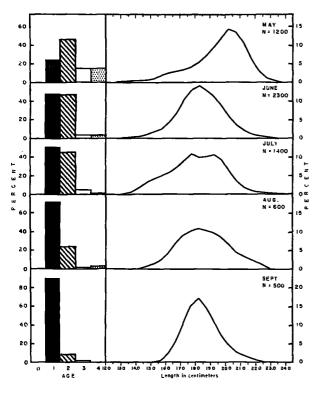


FIGURE 20.—Age and length composition of the summer purse-seine catch at Beaufort, N. C., 1955.

several locations were comprised of successively smaller fish as the season advanced. This was especially the case in 1952 and 1953 when most of our samples were obtained from purse-seine catches landed at Lewes, Del. When fish assigned to the 1951 ring class began to decline in the catches at Lewes in midsummer of 1954, sampling was extended northward to Port Monmouth, N.J., and Amagansett, N.Y., where this ring class dominated the catches.

The location of fishing also shifts frequently during the purse-seine season, depending on the availability of fish; hence, our samples may not have been truly representative of a given ring class over its entire range of distribution. As an example, the 1951 ring class was known to range from northern New Jersey to the northern Gulf of Maine during the summer of 1955. Although purse-seine fishing for Atlantic menhaden occurred no farther north than Casco Bay, Maine, that year, a few samples of this ring class were obtained from catches taken incidentally by weirs as far north as the Bay of Fundy. The northernmost fish of this group, therefore, were not well represented in our summer samples. Also, fishing activities of the purse-seine fleet in southern New England waters shifted markedly throughout the 1955 season, ranging from Long Island Sound to Massachusetts Bay. Thus, when fishing concentrated for a time in Long Island Sound, larger fish of the 1951 ring class which occurred in Cape Cod waters may not have been well represented in our samples. Our data, therefore, cannot be assumed to represent completely the growth of the scales of fish of the 1951 ring class over its entire range.

A further apparent discrepancy noted in the curves was that a number of the distributions appear to be bimodal, especially those of the first year's scale growth in fish of the 1952 ring class. It might be that the two size groups suggested in the first year's scale growth represent fish belonging to different subpopulations (June 1958) or growth differences resulting from differential spawning.

MARGINAL SCALE GROWTH

Recognition of a newly formed age ring on the scales was based on the appearance of a narrow, clear band on the edge of the sculptured, anterior field. It is discernible earliest in the lateral areas adjacent to, and outside, a relatively wide, darker zone of regularly spaced ridges. It later becomes apparent anteriorly and, at this stage, may be traced around the entire sculptured portion of the scale.

To determine the time of year during which new rings formed on the scales, measurements of the projected scale image of the new growth zone, i.e., the distance from the last submarginal ring to the edge of the scale, were recorded when they approximated or exceeded 0.5 millimeter. Measurements of marginal increments were tabulated for each month for which data were available over a 5-year period, 1952 through 1956, for scales of the 1951 ring class and over a 2-year period, 1954 and 1955, for the 1952 ring class. Percentage frequency distributions of marginal increments, by 3-millimeter size classes, are shown in figure 21.

Scales assigned to ring-class 1951 were first obtained in late June 1952 (scales with 1 ring). It may be seen in figure 21 that they showed rather wide marginal growth zones which progressively increased in width through October.

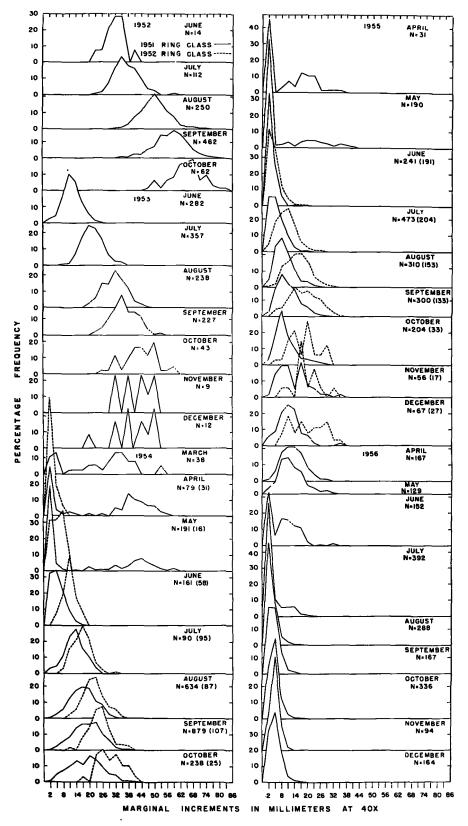


FIGURE 21.-Monthly frequency distributions of marginal increments of scales assigned to ring-classes 1951 and 1952.

In 1953, as 2-ring scales, the marginal zones were narrowest in June and again reached a maximum width in October. Of the scales collected in March, April, and May, 1954, some showed narrow marginal growth zones, but, in addition, scales with wide zones, evident the previous fall, also were present. In April and May the percentage of narrow margins increased, while the percentage of wide margins gradually diminished. By June only narrow marginal increments were evident, indicating that the third ring had formed on all scales, and it occurred at least 0.5 millimeter inside the margin. The new growth zones gradually increased in width as the summer progressed, reaching a maximum by September. An almost identical pattern of marginal growth is observed in 1955 when both narrow and wide growth zones were represented on the scales obtained in April. The percentage of narrow marginal growth zones again increased until June, and the modes of their frequency distributions advanced to a maximum in October. In April 1956 the mode of the frequency distribution was nearly identical with that of the previous December; it persisted through May, remained prominent in June, and was still evident in July. By August, however, only scales with narrow marginal growth zones were evident in the collections. This modal size class reached a maximum of only 5 millimeters by September, indicating that by the time the scales assigned to the 1951 ring class showed 5 rings, marginal scale growth was greatly reduced.

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An attempt to follow similarly the growth of scales of this ring class through 1957 (as 6-ring scales) was abandoned when it was found that our grouping of marginal increments by 3-millimeter size classes was too large to show any prominent shift in modal size groups through the season. The average marginal growth by September amounted to only about 3 millimeters.

Except for a few scattered samples, scales assigned to ring-class 1952 first appeared in our collections in April 1954. At that time, they showed 2 rings with narrow marginal increments (shown by the dashed line in fig. 21). The new growth zone increased in width through the summer and reached a maximum in October. In 1955 the first scales of this ring class were obtained in June. The marginal increments were narrowest at that time and gradually increased in width until October.

Although growth from the last submarginal ring to the edge of the scale occurred over an undetermined period of time before it could be measured and recorded, the foregoing findings show conclusively that (1) marginal scale growth was greatest during the warm months of the year, (2) the new ring was apparent earlier on the scales with fewer rings, and (3) formation of a ring occurred once each year and, therefore, must correspond in number with years of life. The data presented in figure 21 further indicate that the new ring was first evident on scales showing from 1 to 4 rings sometime between March and May and somewhat later on scales showing 5 rings.

The protracted period during which ring formation takes place, particularly in older fish, makes it difficult, or even impossible, to determine whether the marginal growth of the scale in some individuals represents a small, but complete, season's growth of the previous year, or exceptionally rapid growth made during the current season. The greatest difficulty, of course, occurs with scale samples obtained in May and June. It is of interest to note that scales of older fish (more than 5 rings) collected in 1955 and 1956 showed the appearance of a submarginal ring commencing in May, and in all age groups, ring formation was completed by late July. The tendency for apparently earlier ring formation in the younger age groups has been reported by other investigators (Hile 1941; Hodgson 1924); however, it must be recognized that scale growth is much slower in older fish, therefore, the new ring may not become visible until later in the season even though it may have been laid down at the same time as in previous years.

Because of the protracted period of ring formation in Atlantic menhaden, it becomes necessary in age analysis to choose some arbitrary date on which a fish is held to pass from one age group into the next. Based on the developmental stages of the gonads and the distribution of near-ripe fish in the catches, Higham (Ms.)¹ has demon-

¹ Joseph R. Higham. MS. Observations on the sexual maturation and spawning of Atlantic menhaden based on ova diameter measurements. Bureau of Commercial Fisheries Biological Laboratory, Beaufort, North Carolina. 1959.

strated that the bulk of spawning occurs from late fall until late spring. Accordingly, it seems reasonable to choose January 1 as the date of transition to the next higher age group. This practice requires that a virtual ring be credited to the edge of the scale from the beginning of the calendar year through the time of new ring formation. Ring classes, hereinafter referred to as year classes, therefore, may be designated according to the calendar year in which spring spawning takes place. Thus a fish caught in February 1955, showing 1 ring and a wide marginal growth zone on its scales would be designated as age 2 and assigned to year-class 1953; and since it could have been hatched any time between roughly November 1952 and June 1953, it may be from 20 to 27 months old at the time of capture.

This method of assigning fish to age groups and year classes has been incorporated into the routine age analysis of menhaden scale readings.

LOCAL DIFFERENCES IN MARGINAL SCALE GROWTH

To determine whether differences in the time of ring formation were indicated in various localities along the Atlantic coast, comparisons were made of marginal increments of scales from fish captured in May and June 1955 and assigned to the 1954, 1953, and 1952 year classes (1, 2, and 3 rings). Scale data are plotted in figure 22. Over the geographical range of each of these year classes represented in the commercial fishery, ring formation was completed sometime prior to May, except for a few individuals of the 1952 year class. Judging from the relative widths of the new growth zones, ring formation in each year class occurred earliest in southern waters and progressively later farther northward. Since the scales were read without knowledge of the locality from which they came, these findings support the conclusion that rings are not formed sporadically, but appear during the spring months. New scale growth varied considerably among individuals, especially in the younger age groups, and this variability is greatest in those fish occurring in southern coastal waters.

Since the menhaden purse-seine fishery commences at varying times and is dependent on different age groups in the different localities along the Atlantic coast, the foregoing findings

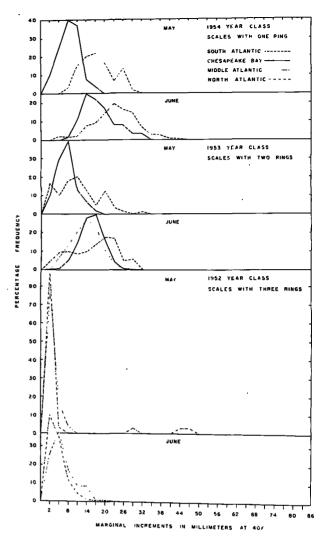


FIGURE 22.—Frequency distributions of marginal increments in scales from fish captured in 1955 and assigned to year-classes 1952 through 1954, from different localities along the Atlantic coast.

are of particular interest. Normally, the season in the southern waters (Beaufort, N.C., to Fernandina Beach, Fla.) begins about the first week in May and is based almost exclusively on the younger age groups, 1- and 2-ring fish predominantly. In Chesapeake Bay and middle Atlantic waters, the fishery normally gets under way during the last week in May. The Chesapeake Bay catch is comprised mostly of 1- and 2-ring fish, whereas 2- and 3-ring fish constitute the bulk of the middle Atlantic catch. In waters north of Long Island, fishing generally begins sometime in June and is based predominantly on older age groups.

The data presented in figure 22 indicate that ring formation in the first three age groups was completed at the onset of the 1955 purse-seine season in all localities. In older age groups, ring formation was completed in most individuals by the time the purse-seine fishery got under way in the northern waters in June. It was shown (p. 337 and fig. 21) that in 1955 the appearance of the new ring on scales of fish of the 1951 year class (4 rings) was completed in all individuals by June; however, by mid-May ring formation was completed in about 70 percent of the scales examined. Of the remaining fish with wide marginal zones on the scales in May, every individual showed the new ring forming, but since new growth was less than 0.5 millimeter of the projected scale image, it was not recorded in our measurements. In 1956 only a small percentage of the fish assigned to the 1951 year class had laid down a complete ring on scales in April and May as shown by the wide marginal growth zones (fig. 21). Although both narrow and wide increments were represented in our data in June and July, 56 percent of the scales examined in June and 86 percent of those in July showed the new ring completely formed. New scale growth was apparent on all scales examined in July, even though it was less than 0.5 millimeter on some of the scales and, therefore, was not recorded.

AGREEMENT IN PARALLEL READINGS

It was noted earlier (p. 324) that two independent readings were made on all scale samples in the collections. A tabulation of these results indicated a high percentage of agreement between the two readings in the different years, varying between 90.2 and 95.9 percent (table 2). The major portion of the disagreements for all years involved the first ring (51.3 percent). Differences

 TABLE 3.—Number of disagreements in two independent readings of 1955 scale samples resolved in joint readings, according to number of rings

Number of rings	Number of scales examined	Original disagreements resolved in joint readings
0	422 923 2, 934 1, 999 3, 543 654 229 64 15 5 2 96 10, 886	7 34 80 113 165 146 42 10 1 1 1 2

in the interpretation of marginal growth on the scales accounted for a small percentage of the total (8.1 percent). The bulk of the remaining disagreements involved the location and number of rings (39.5 percent), and errors in measurements comprised about 1 percent of the disagreements.

A summary of the original disagreements, according to the number of rings, which were encountered in reading the 1955 scale samples and resolved in the joint readings, is presented in table 3. Application of a chi-square test to the data leads to the conclusion that the different age groups did not contribute equally to the disagreements $(a^2 = 50.26; P < 0.001)$. Examination of the data indicated that the disagreements were proportionately higher in the older fish. Further consideration of the disagreements in the last five age groups indicated that more than 97 percent involved a choice of two adjacent rings, or uncertainty of the existence of only one of the rings. The remainder involved uncertainty as to the presence of more than one ring.

From the results of final disposition in the joint readings (last column, table 2), only a small

TABLE 2.—Agreement in age readings of Atlantic menhaden scales collected from 1952 through 1955

		Independent readings			Joint readings				Final disposition				
Year	Number of scales examined	Agreement		Disagreement		Agreement		Disagreement		Agreement		Illegible	
		Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent '
1952 1953 1954 1955	1, 662 1, 585 4, 222 10, 886	1, 575 1, 429 4, 050 10, 189	94, 8 90, 2 95, 9 98, 6	87 156 172 697	5. 2 9. 8 4. 1 6. 4	67 140 - 80 601	77. 0 89. 7 46. 5 86. 2	20 16 92 96	23. 0 10. 3 53. 5 13. 8	1, 642 1, 569 4, 130 10, 790	98, 8 99, 0 97, 8 99, 1	20 16 92 96	1.2 1.0 2.2 0.9

¹ Includes approximately two-thirds of the 1955 data.

percentage of the total number of scales in each year was rejected as illegible. The higher percentage in 1954 was due largely to the discarding of scales in which mold formation obscured the sculptured pattern in the central portion of the anterior field. In 1955, scales were stored in a dehumidified room, and loss of material from this cause was precluded.

Although the number of errors represented in the final determinations is difficult to measure, the high percentage of agreement in the two independent readings indicates that recognition of the number and location of the defined age rings must have been based on similar, objective criteria. To minimize reading errors, we routinely have continued the practice of two independent readings of all scale samples, followed by a joint reading of those scales on which there is disagreement.

SCALES FROM FISH OF KNOWN AGE

Final evidence of the validity of scale rings as age indicators in Atlantic menhaden is furnished from fish of the 1955 year class reared at the U.S. Fishery Laboratory, Beaufort, N.C. Material for this study was collected in the Neuse River, North Carolina, on July 15 and 22, 1955. The fish were obtained with a beach seine and transported in a live car to an outdoor rearing pond. About 500 individuals, ranging from 74 to 93 millimeters in length, were transplanted successfully. Natural food was introduced continuously into the rearing pond by means of a circulating system which pumped water from the adjacent sound. Heavy predation by wintering herring gulls resulted in a high mortality during December 1955 and January 1956, and by the end of the winter the original number had been reduced by more than one-half. The pond was drained and the remaining 64 fish were removed on September 27, 1956, after 14 months of confinement.

Samples of fish were preserved at the time of transplantation and periodically throughout the rearing period. Scales were removed from all preserved specimens and examined for growth characteristics. None of the scales showed any indication of ring formation before March 18,

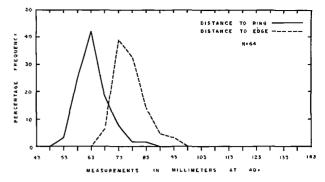


FIGURE 23.—Frequency distributions of scale measurements on 64 fish removed from a rearing pond at Beaufort, N. C., at the end of 14 months impoundment.

1956, when 20 of 54 specimens examined showed either a complete ring just inside the margin of the scale or traces of the new ring being formed in the lateral fields. On April 19 an additional 72 specimens were removed and all but 18 individuals showed a completely formed ring; however, an incomplete ring was discernible on all scales of the group. A sample was taken on May 2, and formation of the first ring on the scales had been completed in all specimens.

Scale measurements made on the 64 specimens removed at the end of the impoundment period are shown in figure 23. Without exception, only 1 ring was present on the scales. A single mode occurs in the length frequencies of the first year's scale growth, followed by a single mode in the curve representing scale growth in the second year of life.

These results show that only one ring was formed on the scales of Atlantic menhaden impounded over a 14-month period and that it is a reliable age mark. This experiment further demonstrated that the onset of ring formation on the scales varies among individuals, but is completed between March and May.

SUMMARY

1. Scales for ascertaining the validity of rings as age indicators were obtained from 13,510 juvenile and adult Atlantic menhaden taken in gill-, pound-, and fyke-net, purse-seine, and beach-seine catches. From 1952 through 1954, scale samples were obtained along the middle Atlantic coast of the United States. In 1955 scales were collected over the range of the commercial fishery from Portland, Me., to Fernandina Beach, Fla.

2. Scales of menhaden may be differentiated from those of most other herringlike fishes by the serrate or pectinate posterior margin. The anterior field is sculptured with ridges running more or less parallel to the anterior margin.

3. Scales were examined and measurements made of the distances from the proximate center of the base of the sculptured field to each ring and to the margin of the scale with an Eberbach projector at a magnification of $40 \times$. All scales were read at least twice, and differences in the independent readings either were reconciled or the scales discarded.

4. Age rings were identified by the interruptions of the ridges in the sculptured field. Such areas of discontinuous ridges form light bands which are parallel to the margin and occur in the same relative position on all except regenerated or damaged scales of an individual fish.

5. The principal argument for the validity of rings as age indicators was based on scale measurements, which were used to trace the growth of the scales over a period of years. Measurements of scales from fish arbitrarily assigned to the 1951 and 1952 ring classes demonstrated the occurrence of one or more homologous, dominant modes in monthly frequency distributions. The data further showed that (a) each new ring on the scales persisted in the same relative position in which it appeared, (b) the scales increased in length with the number of rings, (c) the distance between the last two adjacent ring modes decreased with age, (d) the distance between the last submarginal ring and the margin of the scale increased through the warm months of the year, reaching a maximum in fall, and (e) the modes of the frequency distributions representing newly formed rings were homologous with those of marginal scale growth in the latter months of the previous year.

6. The major discrepancies in the frequency distributions of measurements of scale lengths were (a) failure within a ring class of homologous modes to occur in the same position each month, and (b) a downward shift of modes representing the first and second year's scale growth, both within and between years. These discrepancies were ascribed primarily to inadequate sampling. Different growth rates were demonstrated in scales assigned to two different ring classes.

7. Based on the increase in width of the new growth zone (between the last submarginal ring and the edge cf the scale), it was demonstrated that (a) new scale growth occurred during the warm months of the year, (b) a new ring is apparent earlier in younger fish, and (c) ring formation occurred only once each year, between March and May.

8. Differences in the amount of new scale growth were found in several geographical localities along the Atlantic coast. In general, ring formation was found to occur earliest in southern waters and progressively later farther northward.

9. Comparison of independent interpretation of scales by two readers showed a high percentage of agreement. Of the few disagreements, most involved the first ring. Disagreements were also higher among scales from fish in the older age groups.

10. A further verification of the validity of scale rings as a record of age was based on fish impounded over a period of 14 months. Results showed that only one ring appeared on the scales during this period, and it was formed sometime between March and May.

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