AGE, SIZE, GROWTH, AND CHEMICAL COMPOSITION OF ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*, FROM NARRAGANSETT BAY, RHODE ISLAND

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ABSTRACT

Age and size were determined for 2,015 Atlantic menhaden caught in Narragansett Bay, R.I., during 1976. Atlantic menhaden were predominantly age 2 and age 3, and in all age groups were significantly smaller than fish caught from Long Island Sound to the Gulf of Maine during 1955-71. The chemical composition of the Atlantic menhaden, as determined from analysis of selected subsamples, was ash—10.94, carbon—56.61, and nitrogen—8.03% of dry weight; kilocalories—6.238 per gram dry weight and 7.002 per gram ash-free dry weight; and dry weight—33.4% of wet weight.

Instantaneous annual growth rates during the years 1970-75 were estimated from back-calculated fork lengths and wet weights at the time successive scale annuli were formed. Instantaneous daily growth rates of Atlantic menhaden in Narragansett Bay during 1976 were estimated from the growth of the scale margin beyond the 1976 annulus, and from the increase in mean fork length and wet weight of the fish as the season progressed. Growth rates of age 2 and age 3 Atlantic menhaden in 1976 were considerably greater than the respective average growth rates estimated for previous years, suggesting significant differences in age-specific growth rates of Atlantic menhaden in different regions and different years.

The Atlantic menhaden, *Brevoortia tyrannus*, is a schooling, plankton-feeding clupeid which ranges inshore along the Atlantic coast from Florida to Maine. It makes extensive seasonal migrations, moving north during spring and south during fall (Nicholson 1971, 1972, 1978). Atlantic menhaden are usually present in Narragansett Bay, R.I., from April to November, with peak abundance from June to mid-September. Here we report measurements of age, size, and chemical composition of menhaden caught in Narragansett Bay during 1976. We also report the first calculations of instantaneous growth rates in fork length and wet weight, as measured from scale annuli of individual fish. These data are part of a larger study to determine the energy budget of adult menhaden in Narragansett Bay.

METHODS

Atlantic menhaden were sampled from the catch of two purse seiners, operating from Point Judith, R.I. During 1976, fishing activity fluctuated considerably, according to abundance and availability of Atlantic menhaden in Narragansett Bay. Most of the catch was obtained during early June and from late July to early September. All samples were collected during these two periods, with two additional samples collected on 7 October and one on 4 November.

Random samples of fish from a purse seine set were stored on ice and returned to the laboratory at the end of the day. A total of 2,262 fish were sampled from 24 purse seine sets. An average of 94 fish were collected per set, with a maximum of 2 sets sampled on a given day. About 11% (247 fish) that had regenerated scales, and therefore could not be aged, were excluded from further analysis.

Wet weight and fork length were recorded, and several scales were collected for age determination (June and Roithmayr 1960). Every fifth fish from each sample was collected into a subset of five fish and frozen for dry weight determination or chemical analysis. Dry weights, for the calculation of wet weight:dry weight ratios, were determined by drying groups of these frozen fish at 105°C to constant weight. Fish used for chemical analysis were homogenized, while still frozen, with an equal volume of distilled water. Ash, carbon, nitrogen, and caloric contents were determined for subsamples of the freeze-dried homogenate. The ash content was measured by combusting samples at 475°C

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for 4 h (4-8 replicates). The carbon and nitrogen contents were determined with a Hewlett-Packard[2] Model 185B CHN Analyzer (3 replicates) and the caloric content with a Parr adiabatic bomb calorimeter (4 replicates).

Five scales from each fish were mounted dry between acetate sheets and examined under a Wild M5 dissecting microscope at 18×. Annuli were counted, and distances from the focus to each annulus and to the scale margin were measured with an optical micrometer on the most symmetrical and clearly marked scale.

Condition factor (CF) was calculated from the following equation:

$$CF = \frac{\text{wet weight (g)} \times 10^5}{\text{fork length (cm}^3)}. \tag{1}$$

Length-weight relationships were determined from functional regression of $\log_{10}$ wet weight on $\log_{10}$ fork length (Ricker 1973, 1975b; Jolicoeur 1975). Functional regressions were used because experimental error existed in both the x and y values. Growth of the fish during 1976 was determined by regressing the size of the fish (y) against the date of capture (x). Here, ordinary regressions were used because error was associated only with the y values.

TABLE 1.—Size and condition of Atlantic menhaden caught in Narragansett Bay, R.I., during 1976, compared with those caught in the North Atlantic during 1955-71. Means and 95% confidence limits are shown for the Rhode Island data. Size of menhaden during the years 1955-71 are taken from June and Reintjes (1959, 1960); June (1961); June and Nicholson (1964); Nicholson and Higham (1964a, b, 1965a, b); Nicholson (1975).

	Narragansett Bay All fish	North Atlantic	
	3 June-4 Nov.	1955-62	1955-71
Age 1			
Fork length (mm)	233		
Wet weight (g)	238		
Condition factor	1.87		
No. of fish	2		
Age 2			
Fork length (mm)	233±1.5	272	268
Wet weight (g)	241±4.8	363	—
Condition factor	1.86±0.011	1.89	—
No. of fish	633		
Age 3			
Fork length (mm)	238±1.4	296	288
Wet weight (g)	260±3.6	452	—
Condition factor	1.89±0.008	1.89	—
No. of fish	1,224		
Age 4			
Fork length (mm)	249±3.7	312	306
Wet weight (g)	303±14.4	545	—
Condition factor	1.91±0.023	1.90	—
No. of fish	134		
Age 5			
Fork length (mm)	272±10.3	321	317
Wet weight (g)	384±39.7	604	—
Condition factor	1.89±0.068	1.90	—
No. of fish	18		
Age 6			
Fork length (mm)	274±1.2	329	325
Wet weight (g)	407±1.6	657	—
Condition factor	1.94±0.295	1.91	—
No. of fish	4		

RESULTS AND DISCUSSION

Atlantic Menhaden Age Structure, Size, and Condition Factor

Atlantic menhaden taken from Narragansett Bay during 1976 were predominantly age 2 and age 3 (Table 1), and the relative proportions of the different age groups in the catch remained approximately constant throughout the sampling period. The high proportion (31.4%) of age 2 menhaden taken in the Narragansett Bay catch during 1976 was unusual, based on records from previous years. During 1955-71, age 2 menhaden usually did not migrate in significant numbers north of Long Island, although in some years large numbers were observed in New England waters (June and Reintjes 1959, 1960; June 1961; June and Nicholson 1964; Nicholson and Higham 1964a, b, 1965a, b; Nicholson 1975). Also, the age distribution in the 1976 Narragansett Bay catch (Table 1) was quite different from that in 1975 (Ganz 1975), where, in a sample of 1,100, age 1 = 0.2%, age 2 = 14.6%, age 3 = 70.7%, age 4 = 13.4%, and age 5 = 1.6%.

Age 4 and older menhaden contributed significantly in numbers and in biomass to the North Atlantic catch prior to 1966 (Nicholson 1975). However, during the mid-1960's these older age groups dwindled until they became a negligible part of the catch (Nicholson 1975). Small numbers of age 4+ menhaden in Narragansett Bay catches of 1975 (15.0%) and 1976 (7.7%) indicate that the relative abundance of these age groups continues to be low.

Menhaden caught in Narragansett Bay in 1975 (mean weight 297.6 g (Ganz 1975)), and in 1976 (this study), were considerably smaller than fish of the same age caught during 1955-71 in the North Atlantic area (Long Island Sound to Gulf of Maine) (Table 1). However, the condition factor of the 1976 fish was similar to that of fish previously caught in the North Atlantic (Table 1), implying that the basic length-weight relationship was the same.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

The relationship between wet weight and fork length in the 1976 fish was determined by regressing $\log_{10}$ wet weight on $\log_{10}$ fork length. The functional regressions determined for age groups 2-5 were not significantly different in slope or elevation ($P<0.05$), and a common relationship for all ages combined was therefore determined; where W = wet weight (g) and L = fork length (mm):

$$\log_{10} W = -5.3055 + 3.2441 \log_{10} L \quad (2)$$
$$r = 0.9615$$
$$n = 2{,}015.$$

Back-Calculated Size-at-Age and Growth Rate

The fork length, at the time a menhaden formed each of its scale annuli, was calculated by direct proportion by:

$$\frac{L_i}{S_i} = \frac{L_c}{S_c} \quad (3)$$

where L_i = fork length (mm) at the time scale annulus i was formed
S_i = width of scale (mm) from focus to annulus i
L_c = fork length (mm) of the fish at time of capture
S_c = width of scale (mm) from focus to outer margin, at time of capture.

Mean back-calculated fork lengths of each age group at the time of annulus formation are presented in Table 2. The overall length-weight relationship (Equation (2)) was used to convert the back-calculated fork lengths of each fish to wet weight; mean values for each age group are presented in Table 2.

These back-calculated lengths and weights were then used to calculate the annual instantaneous growth rate of each fish during previous years (Table 3), where

$$G_i(L) = \log_e L_{(i+1)} - \log_e L_{(i)} \quad (4)$$

where $G_i(L)$ = instantaneous yearly growth rate

TABLE 2.—Mean back-calculated fork length and wet weight of Atlantic menhaden caught in Rhode Island waters during 1976, using the overall length-weight relationship (Equation (2)).

Age (1976)	Year class	n	Mean ± 95% confidence limit, back calculated at annulus at age 1	2	3	4	5	6
Fork length:								
2	1974	633	103.5±1.9	179.0±1.2				
3	1973	1,224	91.4±1.0	150.8±1.0	191.3±1.0			
4	1972	134	90.4±3.2	146.5±3.9	185.0±4.0	217.3±4.6		
5	1971	18	100.9±10.3	161.4±10.6	193.5±11.6	220.7±13.2	248.5±12.5	
6	1970	4	114.2±18.7	163.9±30.6	186.6±34.6	214.6±36.4	236.7±48.2	252.0±52.5
Wet weight:								
2	1974	633	20.4±1.2	103.5±2.4				
3	1973	1,224	13.1±0.5	60.9±1.4	129.1±2.5			
4	1972	134	12.8±1.8	57.3±5.0	118.7±8.4	199.7±14.0		
5	1971	18	18.0±6.2	76.2±15.2	136.1±25.9	208.4±37.4	302.0±45.5	
6	1970	4	24.1±12.1	78.4±42.5	119.4±70.9	186.9±95.6	260.6±170.1	319.5±208.7

TABLE 3.—Mean annual growth in fork length (L)[1] and in wet weight (W)[2] of each age group of Atlantic menhaden during previous years. These individual growth rates were then averaged to provide an estimate of the mean growth of each age group during successive years of its life.

Age (1976)	Year class	n	Mean ±95% confidence limit, instantaneous yearly growth at age 1	2	3	4	5
Fork length:							
2	1974	633	0.5745±0.0189				
3	1973	1,224	0.5129±0.0092	0.2406±0.0047			
4	1972	134	0.4906±0.0267	0.2385±0.0148	0.1608±0.0103		
5	1971	18	0.4814±0.0923	0.1831±0.0408	0.1313±0.0244	0.1207±0.0269	
6	1970	4	0.3600±0.1317	0.1299±0.1024	0.1407±0.1479	0.0964±0.0525	0.0620±0.0282
Wet weight:							
2	1974	633	1.8636±0.0614				
3	1973	1,224	1.6639±0.0300	0.7805±0.0152			
4	1972	134	1.5917±0.0865	0.7737±0.0480	0.5218±0.0335		
5	1971	18	1.5617±0.2993	0.5941±0.1325	0.4260±0.0791	0.3917±0.0872	
6	1970	4	1.1678±0.4272	0.4213±0.3322	0.4563±0.4799	0.3128±0.1702	0.2011±0.0914

[1]Growth was calculated individually for each fish from its back-calculated fork length at the time of annulus formation in 2 successive years, where instantaneous yearly growth rate, $G_i(L) = \log_e L_{(i+1)} - \log_e L_{(i)}$

[2]Growth was calculated individually for each fish from its back-calculated wet weight at the time of annulus formation, where instantaneous yearly growth rate, $G_i(W) = \log_e W_{(i+1)} - \log_e W_{(i)}$.

in fork length for a fish age i

$L_{(i)}$ = back-calculated fork length at the time annulus i was formed

$L_{(i+1)}$ = back-calculated fork length at the time annulus $i+1$ was formed.

The instantaneous annual growth in wet weight, G_i (W), was similarly calculated from back-calculated wet weight of each fish at the time each annulus was formed (Table 3).

Growth calculated in this way is the "true growth rate" of the individual fish, as opposed to the "population growth rate" derived from the mean size-at-age of a fish population and which generally underestimates the true rate (Ricker 1975a). However, individual growth rates calculated according to Equation (4) may still underestimate growth of the average individual in prior years, if the back-calculations of size-at-age are affected by Lea's Phenomenon. Although Lea's Phenomenon has been observed in menhaden (June and Roithmayr 1960; Nicholson 1972), we are unable to assess the importance of this potential bias in Tables 2 and 3, because we lack the necessary information on actual mean size and seasonal growth rates of the menhaden population during 1970-75.

Among age groups 3-6 (1970-73 year classes), the mean back-calculated size-at-age and the annual instantaneous growth rates of fish of equivalent age were not significantly different (P<0.05) (Tables 2, 3). Annual growth rates declined with increasing age of the fish. The mean back-calculated size-at-age of age 2 menhaden (1974 year class) was, however, significantly larger (P<0.05) than that of fish of earlier year classes (Table 2), indicating that age 2 menhaden had grown significantly more at age 0 and age 1 than fish from the older age groups.

Further information on total menhaden population movements and on age and size structure during 1976 is needed in order to evaluate the Narragansett Bay data in terms of the population as a whole. However, some preliminary conclusions may be drawn, based on comparisons with data from 1955 to 1971.

The summer distribution of the Atlantic menhaden is discontinuous, with a southern group ranging from Florida to Virginia and a northern group (composing the main body of the population) ranging from Chesapeake Bay to Maine (June and Reintjes 1959, 1960; June 1961; June and Nicholson 1964; Nicholson and Higham 1964a, b, 1965a, b; Nicholson 1971, 1975). During summer the northern group is age-stratified along the coast, with younger fish in the more southern part of the range and older fish predominating in the north. Nicholson (1971) concluded that age 1 menhaden were most abundant from Chesapeake Bay to New Jersey; age 2 from New Jersey to the south shore of Long Island; age 3 from Long Island Sound to Nantucket Sound; and age 4+ from Nantucket Sound to Maine. The average size of individuals within each age group also increased with latitude, especially with age 1 and age 2 fish. This size stratification was much less pronounced for age 3 and older menhaden.

Since Rhode Island is located within the summer population center of age 3 menhaden, Rhode Island landings should provide a good estimate of the mean size of age 3 menhaden in the population. However, since Rhode Island is near the northern limit of the age 2 fish, we would expect the landings to represent only the larger members of this age group.

Records from 1955 to 1971 suggest that age 2 menhaden caught in Narragansett Bay during 1976 were probably the larger members of the 1974 year class and were not representative of the year class as a whole. The comparatively large size-at-age and the growth rates back-calculated for the age 2 menhaden at age 0 and age 1 (Tables 2, 3) are consistent with this suggestion.

Menhaden of all ages (including age 2) caught in Narragansett Bay during 1976 were among the smallest fish for their age ever recorded, and resembled the very small menhaden typically caught in Chesapeake Bay in earlier years (June and Reintjes 1959, 1960; June 1961; June and Nicholson 1964; Nicholson and Higham 1964a, b, 1965a, b; Nicholson 1971). The back-calculated fork lengths of the 1976 fish demonstrated that they had been small since age 1. Size differences between age groups were also greatly reduced (Tables 1, 2, 3).

The reason for the small size of menhaden caught in Narragansett Bay during 1975 and 1976 is not known. Present results are open to two interpretations: 1) Migratory patterns during 1976, and possibly 1975, did not follow the pattern observed in earlier years, and therefore the size of the menhaden from Narragansett Bay was not representative of any age group in the overall population; or, 2) there has been a significant, overall reduction since 1971 in size-at-age within the Atlantic menhaden population. Such a reduction in size-at-age could result from a number of factors, including poor growth during age 0 only, followed by normal growth rate; an overall decline in the mean growth rate of all age groups; or a shift in the relative proportions of different spawning groups within the population (see June 1965; Nicholson 1972), where faster growing individuals have declined and been replaced by slower growing individuals.

Growth During 1976

Instantaneous Daily Growth Rate

Mean instantaneous daily growth rates of menhaden caught in Narragansett Bay during 1976 were estimated from the seasonal increase in mean size of the fish. Such estimates, based on successive samples from a population, assume that the fish were initially of similar size and that there was no significant influx of new fish, with different growth histories, into the region during the study period; these conditions are difficult to meet with a free-ranging fish such as the menhaden. However, we have evidence that these conditions were met, at least for a 1-mo period during the study. First, back-calculated fork lengths at the most recent annulus indicated that menhaden caught in Narragansett Bay were of similar length at the start of the 1976 growing season (Fig. 1). Second, daily observations by the menhaden spotter pilots suggest that our samples collected between 3 August and 1 September were derived from a single group of menhaden. Many large schools were observed moving into Narragansett Bay during the week of 26 July. No significant additional movement of schools into or out of the bay was observed until 7 September, when large schools were again seen entering the bay. Uniformity of the back-calculated fork lengths of the menhaden sampled during this period (Fig. 1) supports the fishermen's opinion that the same group of fish was being sampled. The influx of new fish into the area, observed by the commercial fishermen on 7 September, was accompanied by an abrupt shift in the mean and variance of back-calculated fork lengths of age 3 menhaden on 7-8 September, presumably because of the mixing of new arrivals with those already present (Fig. 1).

Daily growth rates of age groups 2 and 3, the most abundant age groups in the samples, were estimated for the period 3 August-1 September

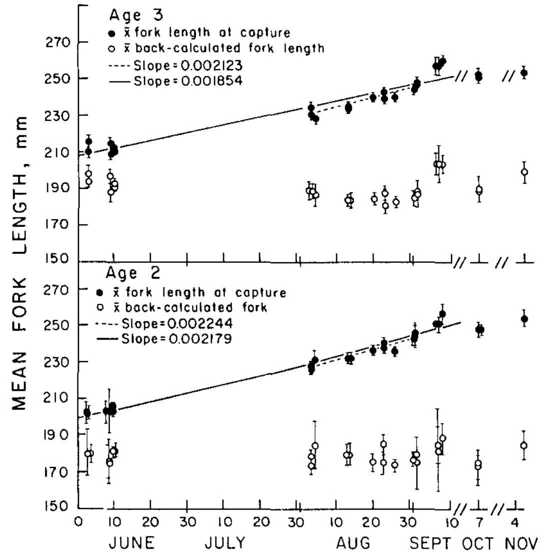

FIGURE 1.—Mean fork length ±95% confidence limits of Atlantic menhaden collected from Narragansett Bay during 1976. Curves depict the instantaneous daily growth in length (Table 4, Equations (9)-(12)).

from 1) rates of increase in mean fork length and wet weight during this period (Figs. 1, 2) and 2) growth rate of the scale margin beyond the 1976 annulus (Fig. 3).

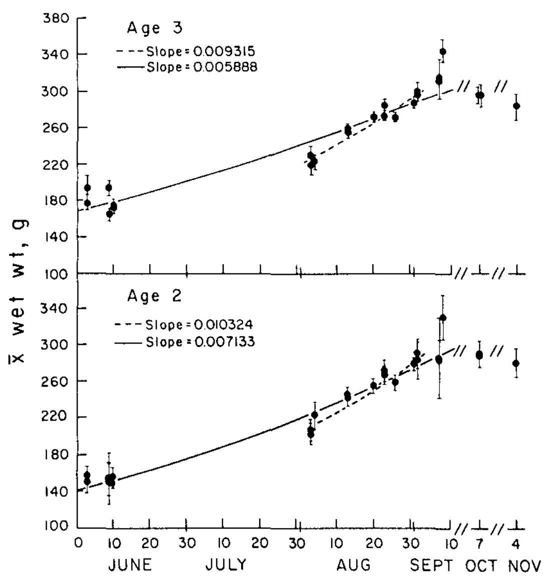

FIGURE 2.—Mean wet weight ±95% confidence limits of Atlantic menhaden collected from Narragansett Bay during 1976. Curves depict the instantaneous daily growth in wet weight (Table 4, Equations (13)-(16)).

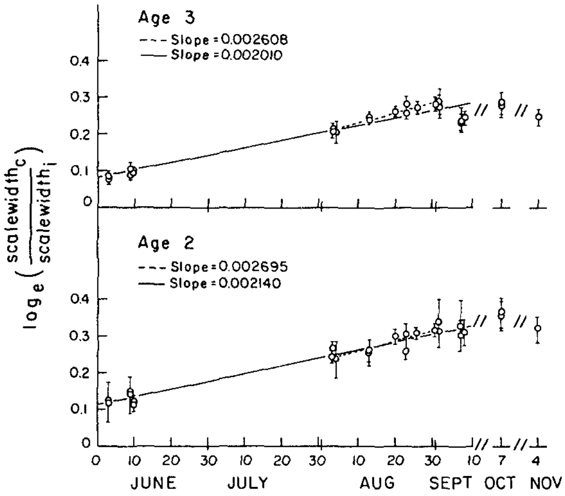

FIGURE 3.—Seasonal growth of the scale margin beyond the 1976 annulus in Atlantic menhaden collected from Narragansett Bay during 1976. Means ±95% confidence limits are shown. Curves depict the instantaneous daily growth of the scale margin (Table 4, Equations (5)-(8)).

Growth rates in fork length and wet weight were determined by regressing $\log_e$ fork length and $\log_e$ wet weight vs. the date of capture (Figs. 1, 2; equations are in Table 4). Mean instantaneous daily growth rates were equal to the slopes of the relationships. Growth of the scale margin was determined for each fish from

$$G = \log_e \frac{S_c}{S_i} \tag{4}$$

where G = instantaneous growth increment
S_c = total width (mm) of the scale at time of capture
S_i = width (mm) to the most recent (1976) annular ring.

The value of G provides an independent estimate of the total amount of growth by that fish during 1976, up to the time of capture. If the exact date were known when fish resumed growth during the spring of 1976, the mean daily growth rate for the entire season could be determined for each individual fish. However, since this date is unknown, the mean daily growth rate can be estimated only for the overall population, by repeatedly sampling that population and regressing the individual values of G against the date of capture (Fig. 3). This approach is analogous to that already described for estimating daily growth in fork length and wet weight.

Instantaneous daily growth rates of age 2 and age 3 menhaden caught within the bay during 3 August-1 September were 0.27 and 0.26%/d in the growth of the scale margin, 0.22 and 0.21%/d growth in fork length, and 1.03 and 0.93%/d growth in wet weight (Table 4). There were no significant differences ($P<0.05$) between these measures of growth for age 2 and age 3 menhaden, probably because the two age groups were very similar in size. The mean daily growth rate of the scale margin did not differ significantly ($P<0.05$) from that of fork length, indicating that both grew in the same proportion.

Daily growth was also estimated, as described above, for all fish collected between 3 June and 8 September (Table 4). These growth estimates were lower than those derived from fish thought to have remained within the bay during August, but only growth estimates in wet weight were significantly different ($P<0.05$).

TABLE 4.—Linear regressions from which the instantaneous daily growth rates of Atlantic menhaden in Narragansett Bay during 1976 may be calculated, where x = date of capture (1 June = day 0 and 8 Sept. = day 100) and (A) $y = \log_e\left(\frac{\text{scale width}_c}{\text{scale width}_i}\right)$; (B) $y = \log_e$ fork length (mm); and (C) $y = \log_e$ wet weight (g). y values are the means of each sample of fish; n = the number of samples. The instantaneous daily growth rate equals the slope of each regression relationship.

	Regression statistics									
	Age 2					Age 3				
	Eq. no.	Intercept	Slope±95% C.L.	r	n	Eq no.	Intercept	Slope±95% C.L.	r	n
(A) Growth of scale margin										
3 June-8 Sept.	(5)	0.11201	0.002140±0.000203	0.9810	21	(6)	0.08157	0.002010±0.000265	0.9641	21
3 Aug.-1 Sept.	(7)	0.06990	0.002695±0.001058	0.8767	12	(8)	0.04600	0.002608±0.000562	0.8767	12
(B) Growth in fork length										
3 June-8 Sept.	(9)	5.29509	0.002179±0.000147	0.9902	21	(10)	5.33835	0.001854±0.000225	0.9693	21
3 Aug.-1 Sept.	(11)	5.28420	0.002244±0.000490	0.9541	12	(12)	5.30698	0.002123±0.000520	0.9468	12
(C) Growth in wet weight										
3 June-8 Sept.	(13)	4.96608	0.007133±0.000638	0.9830	21	(14)	5.12665	0.005888±0.000815	0.9606	21
3 Aug.-1 Sept.	(15)	4.69906	0.010324±0.001949	0.9650	12	(16)	4.82850	0.009315±0.001729	0.9660	12

The mean dates on which growth was initiated during 1976 were calculated as 10 April and 21 April for age 2 and age 3 menhaden, respectively (Equations (5) and (6) in Table 4). These estimates fell within the time period (March-early May) during which growth is believed to resume and the annular ring is formed (June and Roithmayr 1960).

Seasonal Growth Rate

In addition to these short-term estimates of daily growth rate described above, the total seasonal growth increment was determined for individual fish from the amount of growth of the scale and from back-calculations of growth in fork length and wet weight, since the 1976 annulus was formed. By early June, age 2 and age 3 menhaden had already grown considerably since their 1976 annulus was formed (Table 5). Age 2 menhaden had grown more in length and weight, and showed a greater exponential increment in size, than age 3 menhaden. These results mean that during the spring of 1976, either the age 2 fish had a higher instantaneous daily growth rate than age 3 menhaden, or they resumed growth in the spring earlier than the age 3 fish, or both.

TABLE 5.—Seasonal growth of age 2 and age 3 Atlantic menhaden caught in Narragansett Bay during 1976. Absolute growth (in mm fork length and g wet weight), and the instantaneous growth increment since the formation of the 1976 annulus are shown.

Date of capture	Age 2 $\bar{x}$±95% C.L.	Age 3 $\bar{x}$ ±95% C.L.
3-10 June		
fork length at capture (mm)	203.7±1.5	212.2±1.2
back-calculated fork length at 1976 annulus (mm)	180.3±1.9	193.3±1.4
growth (mm)	23.4	18.9
exponential increment	0.1220	0.0933
wet weight at capture (g)	153.0±3.9	179.0±3.9
back-calculated wet weight at 1976 annulus (g)	102.0±3.6[1]	132.4±3.1[2]
growth (g)	51.0	46.6
exponential increment	0.4055	0.3016
8 September		
fork length at capture (mm)	247.9[3]	250.6[4]
back-calculated fork length at 1976 annulus (mm)	179.0±1.2[5]	191.3±1.0[5]
growth (mm)	68.9	59.3
exponential increment	0.3256	0.2700
wet weight at capture (g)	292.8[6]	303.5[7]
back-calculated wet weight at 1976 annulus (g)	101.0±2.4[1]	130.5±2.4[2]
growth (g)	191.8	173.0
exponential increment	1.0644	0.8440

[1]Using the length-weight relationshp for age 2 menhaden, where $\log_{10}$ fork length = −5.4799 + 3.3166 $\log_{10}$ wet weight, r = 0.963, and n =633.

[2]Using the length-weight relationship for age 3 menhaden, where $\log_{10}$ fork length = −5.2138 + 3.2062 $\log_{10}$ wet weight, r = 0.956, and n =1,224.

[3]Average size on this date (Table 4, Equation (9)).

[4]Average size on this date (Table 4, Equation (10)).

[5]Based on data from all fish (Table 2).

[6]Average size on this date (Table 4, Equation (13)).

[7]Average size on this date (Table 4, Equation (14)).

By 8 September the mean growth of age groups 2 and 3 during 1976 was considerably greater than the average yearly growth rates of age 2 and age 3 menhaden in other years, as estimated from the back-calculations of size-at-age (Tables 2, 3). For example, during 1976 the scale annuli of age 3 menhaden indicated that when these fish were age 2, their total exponential increments in fork length and wet weight (i.e., their instantaneous yearly growth rates) were 0.2406 and 0.7805, respectively. In comparison, by 8 September the mean exponential increments in fork length and wet weight of age 2 menhaden during 1976 were 0.3256 and 1.0644. Similarly, age 4 menhaden caught during 1976 increased in fork length by 0.1608 and in wet weight by 0.5218 as age 3 fish during 1975. During 1976, the increments in fork length and wet weight of age 3 menhaden were 0.2700 and 0.8440 by 8 September. Some additional growth may have taken place after 8 September; June and Roithmayr (1960) found that growth of the scale margin in Atlantic menhaden continued until September or October.

Results indicate that significant differences in the growth rate of menhaden occur, probably because menhaden, found over an extensive geographic area during the summer, experience a wide range of temperature and food conditions that could affect growth. Further investigation into regional and annual differences in the instantaneous growth rates may provide a basis for determining which geographic regions can potentially contribute most to menhaden productivity and could provide considerable insight into ways of maximizing the yield from this fishery.

Chemical Composition

The mean carbon, nitrogen, caloric, and ash contents and dry weight of menhaden from Narragansett Bay are summarized in Table 6. The ratio of dry weight:wet weight remained fairly constant in all samples; otherwise, there was a consistent trend in those fish with a high caloric content toward high carbon content and low nitrogren and ash content as a percent of dry weight (Fig. 4).

Ash, caloric, and moisture contents of the men-

TABLE 6.—Chemical composition of Atlantic menhaden collected from Narragansett Bay, R.I., between 3 June and 8 September 1976. Determinations were made on groups of five fish.

Constituent	$\bar{x}$±95% C.L.	No. of samples
Dry wt:wet wt	0.334 ±0.018	19
Ash, proportion of dry wt	0.1094 ±0.0292	21
C, proportion of dry wt	0.5661 ±0.0671	18
N, proportion of dry wt	0.08028±0.00349	18
Kcal (g dry wt fish)$^{-1}$	6.238 ±1.006	20
Kcal (g ash-free dry wt fish)$^{-1}$	7.002 ±0.942	20

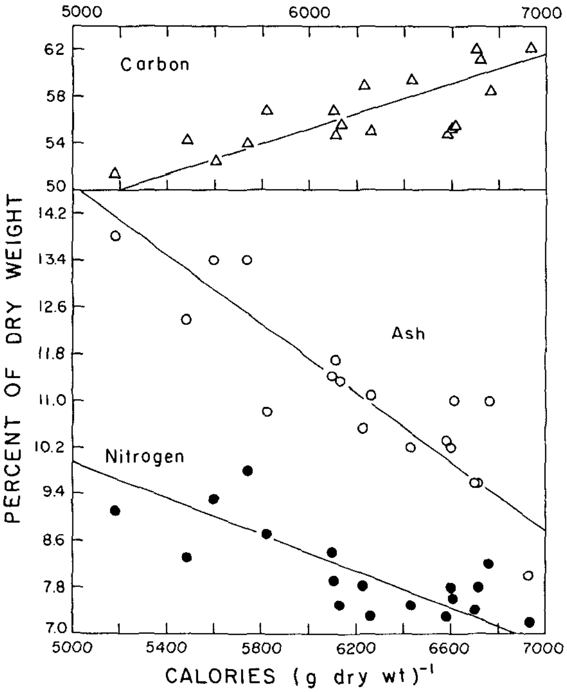

FIGURE 4.—Carbon, nitrogen, and ash contents (percent of dry weight) as a function of caloric content in Atlantic menhaden collected from Narragansett Bay.

haden in the present study are similar to those reported for Atlantic menhaden from Beaufort, N.C., (Thayer et al. 1972) and Chesapeake Bay (Dubrow et al. 1976). Menhaden are comparatively higher in percentage of dry weight and in caloric content than most other fish species (Dahlberg 1969; Perkins and Dahlberg 1971; Mayer et al. 1973; Sidwell et al. 1974; Small 1975; Kitchell et al. 1977; Foltz and Norden 1977).

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LITERATURE CITED

DAHLBERG, M. D.
1969. Fat cycles and condition factors of two species of menhaden, *Brevoortia* (Clupeidae), and natural hybrids from the Indian River of Florida. Am. Midl. Nat. 82: 117-126.

DUBROW, D., M. HALE, AND A. BIMBO.
1976. Seasonal variations in chemical composition and protein quality of menhaden. Mar. Fish. Rev. 38(9):12-16.

FOLTZ, J. W., AND C. R. NORDEN.
1977. Seasonal changes in food consumption and energy content of smelt (*Osmerus mordax*) in Lake Michigan. Trans. Am. Fish. Soc. 106:230-234.

GANZ, A. R.
1975. Observations of the Narragansett Bay menhaden fishery. R.I. Dep. Nat. Resour., Div. Fish Wildl., Mar. Fish. Sec. Leafl. 45:1-21.

JOLICOEUR, P.
1975. Linear regressions in fishery research: some comments. J. Fish. Res. Board Can. 32:1491-1494.

JUNE, F. C.
1961. Age and size composition of the menhaden catch along the Atlantic coast of the United States, 1957, with a brief review of the commercial fishery. U.S. Fish Wildl. Serv., Spec. Sci. Rep.—Fish. 373, 39 p.
1965. Comparison of vertebral counts of Atlantic menhaden. U.S. Fish Wildl. Serv., Spec. Sci. Rep.—Fish. 513, 12 p.

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.
1960. Age and size composition of the menhaden catch along the Atlantic coast of the United States, 1956, with a brief review of the commercial fishery. U.S. Fish Wildl. Serv., Spec. Sci. Rep.—Fish. 336, 38 p.

JUNE, F. C., AND C. M. ROITHMAYR.
1960. Determining age of Atlantic menhaden from their scales. U.S. Fish Wildl. Serv., Fish. Bull. 60:323-342.

KITCHELL, J. F., J. J. MAGNUSON, AND W. H. NEILL.
1977. Estimation of caloric content for fish biomass. Environ. Biol. Fish. 2:185-188.

NICHOLSON, W. R.
1971. Coastal movements of Atlantic menhaden as inferred from changes in age and length distributions. Trans. Am. Fish. Soc. 100:708-716.
1972. Population structure and movements of Atlantic menhaden, *Brevoortia tyrannus*, as inferred from back-

calculated length frequencies. Chesapeake Sci. 13:161-174.

1975. Age and size composition of the Atlantic menhaden, *Brevoortia tyrannus*, purse seine catch, 1963-71, with a brief discussion of the fishery. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-684, 28 p.

1978. Movements and population structure of Atlantic menhaden indicated by tag returns. Estuaries 1:141-150.

NICHOLSON, W. R., AND J. R. HIGHAM, JR.

1964a. 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.

1964b. Age and size composition of the 1960 menhaden catch along the U.S. Atlantic coast, with a brief review of the commercial fishery. U.S. Fish Wildl. Serv., Spec. Sci. Rep.—Fish. 479, 41 p.

1965. Age and size composition of the menhaden catch along the Atlantic coast of the United States, 1961, with a brief review of the commercial fishery. U.S. Fish Wildl. Serv., Spec. Sci. Rep.—Fish. 495, 28 p.

1966. Age and size composition of the menhaden catch along the Atlantic coast of the United States, 1962, with a brief review of the commercial fishery. U.S. Fish Wildl. Serv., Spec. Sci. Rep.—Fish. 527, 24 p.

PERKINS, R. J., AND M. D. DAHLBERG.

1971. Fat cycles and condition factors of Altamaha River shads. Ecology 52:359-362.

RICKER, W. E.

1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.

1975a. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can. Bull. 191:1-382.

1975b. A note concerning Professor Jolicoeur's comments. J. Fish. Res. Board Can. 32:1494-1498.

SIDWELL, V. D., P. R. FONCANNON, N. S. MOORE, AND J. C. BONNET.

1974. Composition of the edible portion of raw (fresh or frozen) crustaceans, finfish, and mollusks. I. Protein, fat, moisture, ash, carbohydrate, energy value, and cholesterol. Mar. Fish. Rev. 36(3):21-35.

SMALL, J. W., JR.

1975. Energy dynamics of benthic fishes in a small Kentucky stream. Ecology 56:827-840.

THAYER, G. W., W. E. SCHAAF, J. W. ANGELOVIC, AND M. W. LACROIX.

1973. Caloric measurements of some estuarine organisms. Fish. Bull., U.S. 71:289-296.