tifying the contents of fish stomachs collected in 1977.

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FECUNDITY OF THE ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*

Although some work has been done to determine the time and place of spawning, age of spawning, and fecundity of Atlantic menhaden, *Brevoortia tyrannus* (Higham and Nicholson 1964), no attempt has been made to relate fecundity and age. In this study, I 1) examined the ovaries of fish 1 to 5 yr old collected during autumn 1970, in the vicinity of Beaufort, N.C.; 2) estimated the number of ripening ova in sexually mature fish; 3) calculated the mean number of ova spawned by fish of each age; and 4) determined the reproductive potential and the net reproductive rates for the 1954-63 year classes.

Atlantic menahden, family Clupeidae, constitute a single biological population (Nicholson 1972, 1978; Dryfoos et al. 1973) inhabitating coastal waters from Florida to the Gulf of Maine. It is subjected to an intensive purse seine fishery from Florida to New England. Fish are landed daily at reduction plants and processed into meal, oil, and solubles. Fishing begins in Florida and North Carolina in late April, in New Jersey coastal waters in early June, and in New England waters in late June. Fishing usually ends in mid to late November, except in the vicinity of Beaufort where schools of migrating fish of all ages from northern areas provide an intensive fishery from November to late December or early January.

Atlantic menhaden make extensive coastal movements and during the fishing season are stratified along the coast by age and size. In autumn most fish north of Virginia move southward and by January are concentrated in offshore waters from Cape Hatteras to northern Florida. About mid-March they begin a northward movement and by mid-June are stratified in coastal waters by age and size, the younger and smaller farther south and the older and larger farther north (Nicholson 1971). South of Cape Hatteras and in Chesapeake Bay most fish are ages 1 and 2. Age-2 fish dominate in coastal waters off New Jersey, ages 3 and 4 in Long Island Sound, and age 4 and older north of Cape Cod. Although they may live to age 9, few older than age 6 are caught.

Menhaden spawn in offshore coastal waters where the eggs hatch in 36 to 48 h (Reintjes 1962). Larvae, carried inshore by ocean currents, enter estuaries where they metamorphose to the adult form at about 35 mm total length. Although some spawning occurs in summer and early autumn in Long Island Sound and New England waters—the only areas where fish of spawning age are found during that time — most spawning occurs in the South Atlantic area from January to March and in the Middle Atlantic area from October to December and March to May. Although there appears to be only one spawning cycle each year, evidence is uncertain as to whether Atlantic menhaden are fractional spawners (Higham and Nicholson 1964).

As the population size decreased in the 1960's age structure also changed. Fish older than age 3 became extremely scarce, and most plants in the northern areas that were dependent on older fish closed. By 1969 few fish older than age 4 were landed, even in the North Carolina fall fishery. which traditionally had been dependent on older fish (Nicholson 1975).

Collection and Preparation of Ovaries

Ovaries were collected from 17 November to 29 December 1970 during the North Carolina fall fishery at the same time catches were being sampled routinely for age and size (June and Reintjes 1959). Sampling personnel measured and weighed the fish, removed scales for aging, and removed the ovaries. Only ripening ovaries fitting the

Stage III classification of Higham and Nicholson (1964) were retained. They were blotted on paper towels to remove excess moisture, weighed to the nearest 0.1 g, split longitudinally and turned inside out, and placed in individual jars of Gilson's fluid modified by Simpson (Bagenal 1967). The jars were shaken to liberate all eggs. After the Gilson's fluid was poured off, along with most pulverized ovarian tissue, the ova were washed and decanted in water several times and forced through a sieve to remove remaining fragments of ovarian tissue, spread on large trays covered with paper towels, and dried under incandescent lamps.

Higham and Nicholson (1964) described four stages in the maturation of ovaries. Ovaries in the immature and intermediate stages contain only undeveloped ova; ovaries in the maturing and ripe stages contain developing as well as undeveloped ova. They concluded that only maturing ova ripened during each spawning period. Maturing ova were described as being opaque and yellow and between 0.35 and 0.78 mm in diameter. I followed this description to separate immature from maturing ova. I also measured fecundity by estimating the number of maturing ova in both ovaries. Instead of counting ova in sample sections of the wet ovary, however, I counted ova in two replicate samples of the dried ova that had been separated from connective tissues. Before being weighed, eggs were allowed to equilibrate with air humidity. Each sample was weighed to the nearest 0.01 mg. If both ovaries weighed more than 12 g, two samples, each weighing 1/350 of the total weight, were taken. If the ovaries weighed 12 g or less, two replicate samples, each weighing 0.035 g, were taken, since fecundity would have been difficult to estimate in samples smaller than 0.035 g. Proportional sampling tended to minimize the counting error for a fixed amount of counting effort. Ova in each sample were counted under a stereoscope. The number of ova in both ovaries, N, was estimated by multiplying the number of ova in the two samples, N_s, by the ratio of total dry weight of eggs, W_t, to dry weight of eggs in samples, W_s ($N = N_s W_t / W_s$). To minimize counting error between samples, a coefficient of variation of 3.0% or less was maintained.

Preliminary calculations indicated that fecundity could be estimated with a precision of about 15% if 30 fish were selected randomly from each age-class. The ultimate number in each age-group was age 1, 21; age 2, 34; age 3, 33; age 4, 12; and age 5, 1 (Table 1).

TABLE 1.—Mean number of eggs (thousands) and mean ovary weight (grams), by age, for Atlantic menhaden sampled from the North Carolina fall fishery, 1970.

Age	No. of fish	Mean no. of eggs	Range	C.V.[1] (%)	Mean ovary wt	Range	C.V. (%)
1	21	115.8	26.5-250.7	47	17.9	4.0-43.5	54
2	34	177.4	39.2-368.8	50	30.1	5.0-62.5	55
3	33	302.8	127.7-458.3	30	50.9	21.1-96.9	34
4	12	308.6	142.7-514.0	36	48.5	22.0-74.8	36
5	1	568.4	—	—	90.0	—	—

[1] Coefficient of variation.

Fecundity

The regressions of fecundity on ovary weight, $F = 6{,}908(OW) - 17.937(OW)^2$, and fecundity on total fish weight, $F = 293(TW) + 0.214(TW)^2$, were curvilinear, but fecundity on body weight only, $F = 488(BW)$, was linear. The R^2 values were 0.981, 0.675, and 0.916, respectively. Although the relative merits of predicting fecundity from different variables are debatable (Bagenal 1967), these three models seem less useful than fecundity on age, which can be used to determine reproductive potential and calculate life table estimates, and fecundity on fish length, which can be used to predict the number of eggs spawned by different size classes.

A statistical test failed to support the curvilinear relation implied by a plot of fecundity on age, perhaps because of the few fish in older age-groups. Of the two linear models tested for estimating fecundity at age, I selected $F = 92{,}592(\text{Age})$ as the better estimator ($r^2 = 0.879$; SE slope = 3,440; SE regression = 89,110). It had tighter confidence limits and a higher r^2 than the model $F = a + bL$.

A logarithmic model ($\log F = a + bL$) was selected to describe the curvilinear relation between fecundity and length and was fitted to both my data and the data of Higham and Nicholson (1964) (Figure 1). Values predicted by this model fit observed values more closely over the entire range than those predicted by the nonlogarithmic model ($F = b_1 L + b_2 L^2$). The difference in the slope coefficients of the logarithmic model fitted to the two sets of data was significant ($P<0.001$). Estimated fecundities were in reasonable agreement for fish up to 275 mm, but diverged for large fish. For 350 mm fish the model fitted to Higham and Nicholson data predicted about 1.75 as many ova as the model fitted to my data.

Differences in fish ages or in the time of year fish were collected, or actual changes in fecundity might account for differences in estimates of ova

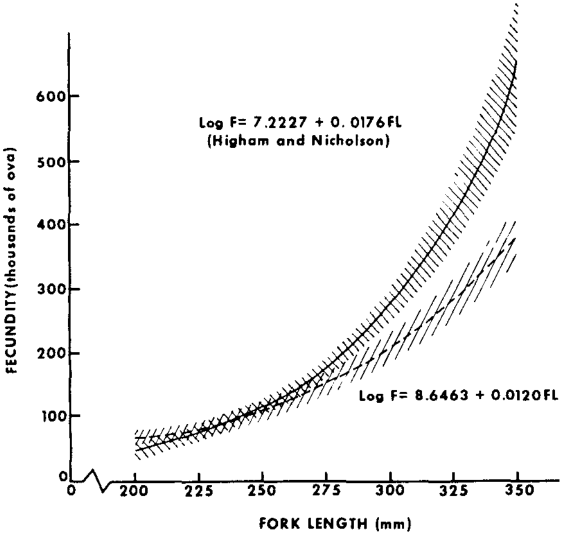

FIGURE 1.—Regression of fecundity on fork length for Atlantic menhaden showing confidence limits on the mean at 95% level. For $\log F = 7.2227 + 0.0176FL, N = 38$, SE regression = 0.3069; SE regression coefficient = 0.0011, $r^2 = 0.726$; for $\log F = 8.6463 + 0.0120FL, N = 101$, SE regression = 0.3330, SE regression coefficient = 0.0007, $r^2 = 0.871$.

for larger fish. Higham and Nicholson (1964), e.g., had four fish with between 400,000 and 500,000 ova, four with between 500,000 and 600,000, and one with over 600,000, whereas from nearly three times as many fish I had only two with over 500,000 and six with between 400,000 and 500,000. I believe, however, that differences in counting techniques caused the differences in ova estimates. I used proportional sampling, whereas they did not. I separated the eggs from each other and from the connective tissue, dried and weighed the eggs, and then counted those in a sample. They counted the eggs in a sample from the wet ovary. Also, a certain amount of subjectivity is involved in distinguishing between maturing and nonmaturing ova.

Reproductive Potential and Net Reproductive Rate

Since the sex ratio of Atlantic menhaden is about equal (Nicholson and Higham 1964), I was able to calculate the annual numbers of females of each age in the population, 1955-68, by dividing half of the number of fish caught at each age by the exploitation rate for all ages (Schaaf and Huntsman 1972). When I collected my material in 1970, recording the maturing stage of fish in catch samples had been discontinued, but Higham and Nicholson (1964) estimated that about 10% of age-1 fish, 90% of age 2, and 100% of age-3 or older fish examined during the North Carolina fall fishery in October-December from 1955 to 1959 had maturing ovaries. From these figures I calculated the number of females of each age that would spawn each year and multiplied it by the mean number of ova spawned by fish of each age to estimate the number of eggs spawned each year (Table 2).

The net reproductive rate, R_0, of a population is defined as the sum of the products of the age-specific survival rate l_x, and the age-specific natality rate m_x, of females (Odum 1971). A value of 1.0 for each generation would indicate that the population is stable and that there is a balance between births and deaths. In fish populations it is nearly impossible to obtain accurate counts or estimates of the number of offspring produced by each age-group. It is possible, however, to estimate the mean number of eggs spawned for fish of each age. If this variable is used for m_x in the formula given by Odum and if $\Sigma l_x m_x$ is called, $R_0{}^*$, then the reciprocal of $R_0{}^*$ should be a rough estimate of the survival rate of female eggs, providing the population is approximately stable. Although the Atlantic menhaden population declined after about 1960, I think in view of the imprecise estimates of other parameters, that it can be assumed stable for the purpose of estimating egg mortality.

$R_0{}^*$ values were calculated for the 1954-63 year classes. I assumed a 0.65 survival rate up to age 1, which I divided into the estimated number of fish that were age 1 (Schaaf and Huntsman 1972) for an estimate of the number of fish at the postlarval stage. Since the sex ratio is equal, this number divided into the estimated number of fish surviving to each age (Schaaf and Huntsman 1972)

TABLE 2.—Estimated number of eggs (multiply by 10^{11}) spawned by Atlantic menhaden, by year and age.

Year	Age in years							Total
	1	2	3	4	5	6	7-9	
1955	83.0	377.6	723.2	119.5	43.6	8.7	3.5	1,359.1
1956	69.7	443.9	103.7	465.1	118.8	31.1	10.7	1,243.0
1957	106.9	136.6	166.7	127.2	144.9	19.7	6.0	708.0
1958	161.1	131.3	51.0	62.8	42.9	28.8	3.0	480.9
1959	73.0	599.2	85.9	40.7	53.0	23.4	10.6	885.8
1960	329.8	205.3	457.9	142.0	59.4	21.1	6.8	1,222.3
1961	44.8	1,938.4	51.2	104.6	12.7	4.3	1.5	2,157.5
1962	57.7	270.2	877.6	85.0	85.0	12.4	3.4	1,391.3
1963	42.2	143.8	88.0	136.6	34.0	13.0	2.6	460.2
1964	38.4	95.3	34.1	19.9	21.0	5.0	1.4	215.1
1965	32.2	108.0	28.2	5.6	4.7	3.4	0.4	182.5
1966	31.2	44.0	9.0	1.1	0.4	0.5	0.2	86.4
1967	20.5	101.1	11.8	1.5	—	—	—	134.9
1968	41.3	91.2	24.7	3.0	0.2	—	—	160.4

yielded age-specific-survival fractions (l_x) for females of each year class. R_0^* for each year class ranged from 7,100 to 25,800 (Table 3). The reciprocal of these numbers, 0.000141 and 0.000039, respectively, indicate a survival rate ranging from 39 to 141 females, or 78 to 282 fish of both sexes, for each 1,000,000 eggs spawned.

Any estimate based in turn on a series of rather imprecise and arbitrary estimates must be viewed with caution, and this one is no exception. Yet it is in line with current knowledge that the survival rate of pelagic fish eggs is extremely low.

TABLE 3.—Net reproductive rates (R_0^*) and their reciprocals ($1/R_0^*$) for the 1954-63 year classes of Atlantic menhaden.

Year class	R_0^*	$1/R_0^*$	Year class	R_0^*	$1/R_0^*$
1954	16,546	0.000060	1959	22,297	0.000045
1955	7,109	0.000141	1960	10,120	0.000099
1956	25,932	0.000039	1961	14,073	0.000071
1957	11,850	0.000084	1962	11,024	0.000091
1958	21,856	0.000046	1963	11,181	0.000089

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ROLE OF LAND AND OCEAN MORTALITY IN YIELD OF MALE ALASKAN FUR SEAL, *CALLORHINUS URSINUS*

The annual commercial harvest of male fur seals has fluctuated widely and declined since the early 1950's. This has occurred despite a fairly stable harvesting regime and efforts to maintain the population near the level believed to be consistent with maximum sustainable productivity (Chapman 1961, 1964, 1973). Variations in early natural mortality are mainly responsible for these changes in the harvest of males which occurs at ages 2-5 yr (mostly 3-4 yr). Kenyon et al. (1954) and Chapman[1] emphasized that natural mortality between birth and age 3 yr is high and that most of it probably occurs during the first winter just after weaning.

This report gives estimates of male survival from natural mortality of pups on land and from the first 20 mo of life at sea, a total interval of approximately 2 yr. The importance of pup numbers and early survival rates in determining annual variations in abundance at age 3 yr is quantified also.

Methods

Data for survival estimates are in Table 1. The age composition of annual kills before 1950 cannot be determined accurately because an aging technique was not available until then (Scheffer

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[1] Chapman, D. G. 1975. Methods of forecasting the kill of male seals on the Pribilof Islands. Background paper for the 19th Annual Meeting of the North Pacific Fur Seal Commission, 10 p. (Unpubl. rep.)