GROWTH AND AGE STRUCTURE OF LARVAL ATLANTIC HERRING, *CLUPEA HARENGUS HARENGUS*, IN THE SHEEPSCOT RIVER ESTUARY, MAINE, AS DETERMINED BY DAILY GROWTH INCREMENTS IN OTOLITHS[1]

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ABSTRACT

Larval Atlantic herring, *Clupea harengus harengus*, were sampled in the Sheepscot River estuary, Maine, using both towed, and buoyed and anchored plankton nets from October 1978 to March 1979, to determine growth rates and age structure. Larval densities and length-frequency distributions, determined from the buoyed and anchored net samples, and the ages of larvae captured in the towed nets, as determined by daily growth increments in the otoliths, showed that there were at least two normally distributed age-groups of larvae which entered the estuary in November and December. The two groups hatched during early October and late November, and each appeared in the estuary when about 4 weeks old. Each of the two age-groups of larvae experienced a reduction in growth rate during the latter half of January and early February. The older of the two groups grew approximately 2.1 mm per week from October to early January and from late February to early March. These older larvae grew little if any, during the midwinter period. The younger of the two groups of larvae showed a similar reduction in growth rate during midwinter and grew about 2.0 mm per week before and about 1.5 mm per week after this period.

Research on larval Atlantic herring, *Clupea harengus harengus* Linnaeus, has been conducted extensively in the western North Atlantic in recent years. This has resulted in numerous accounts of the abundance and distribution of the larvae, as well as estimates of the generalized growth rates. The growth of Atlantic herring larvae in the Gulf of Maine-Bay of Fundy areas has been reported by Tibbo et al. (1958), Tibbo and Legaré (1960), Das (1968, 1972), Sameoto (1972), Graham et al. (1972), and Boyar et al. (1973). These workers used the length-frequency method to determine average growth rates of the larvae. Various studies on the seasonal abundance and size distribution of Atlantic herring larvae have shown that in some years there may be more than one mode in the length-frequency distribution for a particular time and geographical area (Tibbo et al. 1958; Tibbo and Legaré 1960; Das 1968, 1972; Graham et al. 1972; Boyar et al. 1973; Graham in press), indicating multiple spawnings. These polymodal length-frequency distributions of Atlantic herring larvae complicate growth rate estimates since an individual sample may not represent a single homogeneous group of larvae.

A relatively new technique for studying the growth of larval fishes was introduced by Pannella (1971, 1974). He observed daily growth increments in the otoliths of some tropical and low-temperature adult fishes. Brothers et al. (1976) and Struhsaker and Uchiyama (1976) verified the daily nature of these growth increments in several species of larval fishes. Subsequently, others applied this technique to age and growth studies (Ralston 1976; Taubert and Coble 1977; Barkman 1978). Rosenberg and Lough[4] used otoliths to age larval Atlantic herring from Georges Bank. The purpose of our study was to use the otolith aging technique to investigate the growth of Atlantic herring larvae in the Sheepscot River estuary of Maine and to examine the age structure of the larvae entering the estuary.

METHODS

Larval herring were sampled in the Sheepscot River estuary of Maine using both towed, and

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[4]Rosenberg, A. S., and R. G. Lough. 1977. A preliminary report on the age and growth of larval herring (*Clupea harengus* L.) from daily growth increments in otoliths. ICES C.M. 1977/L:26.

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buoyed and anchored plankton nets. Shaw[5] has shown that when used at night there is a little, if any, difference between these gear with regard to catch rates or larval fish avoidance. Only the samples collected by the towed nets were used for otolith analysis. These towed net samples were collected at night on seven occasions from 24 October 1978 to 6 March 1979 using a 1 m, 0.75 mm mesh plankton net. One daytime sample (10 January) was taken with a 61 cm bongo net with 0.505 mm mesh nets on each side. Buoyed and anchored net samples were collected from 5 October 1978 to 27 February 1979 as part of the regular larval Atlantic herring monitoring program conducted by the Maine Department of Marine Resources. The buoyed and anchored nets consisted of six lines of nets fished at four stations in the estuarine channel. Each line had four 0.5 m, 0.75 mm mesh nets, with a digital flowmeter mounted in each net. The nets were set at dusk and retrieved at dawn each sampling date, and fished approximately one semidiurnal tidal cycle. The buoyed and anchored net samples were preserved in 5% Formalin[6] and length-frequency distributions and catch rates for larval Atlantic herring determined. The characteristics and performance of the buoyed and anchored nets were reported by Graham and Venno (1968), Graham and Davis (1971), and Graham (1972).

The larvae from the towed samples were not preserved, but were sorted within 2 h of collection, placed in plastic Petri dishes, and frozen fresh at −18° C for future otolith analysis. The samples were later thawed and each fish measured to the nearest 0.5 mm. Figure 1 shows that the frozen larvae shrink an average of about 1-2 mm more than Formalin preserved larvae. The sagittae, or largest otoliths, from both sides of the head were teased onto a microscope slide under a binocular microscope. The otoliths were mounted in Permount and covered with a glass coverslip. The numbers of daily growth increments in one of each pair of sagittae were counted under a compound microscope at 1,000 × magnification. The increments were counted twice and their mean number computed. Only those otoliths in which there was a difference between counts of 5% or less were used in the analysis. These data were used to estimate daily growth rates and age composition of the larvae. The daily growth increments in larval Atlantic herring otoliths show up very clearly, and only 17 of the 317 larvae examined had otoliths with increments too faint to be counted accurately.

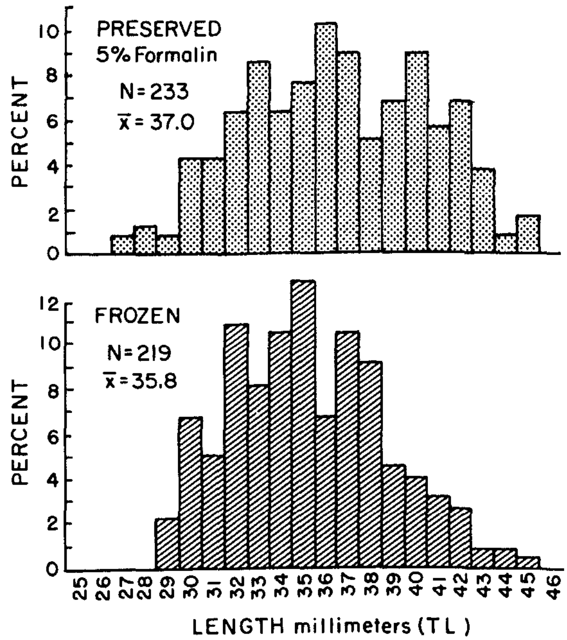

FIGURE 1.—Length-frequency comparison of 5% Formalin preserved versus frozen Atlantic herring larvae captured with 61 cm bongo nets on 4 April 1980 in the Damariscotta River estuary, Maine. Larvae from the starboard net were preserved in Formalin and larvae from the port net were frozen. Measurements were performed 2 mo later. A modified *t*-test (Snedecor and Cochran 1967) showed that the two means were significantly different ($P < 0.01$).

RESULTS

Larval Age Structure

Changes in modal lengths of larvae during autumn and winter indicate that groups of larvae entered the estuary and subsequently lost their identities through differential mortality and growth, since the larvae are not known to depart the estuary once established there (Graham et al. 1972). Length-frequency data from the buoyed and anchored net samples (Figure 2) showed a trimodal length distribution (range 6-30 mm) for larvae present in the Sheepscot River estuary on 19 October. A large group of smaller larvae entered on 2 November when only a trace of the

[5]Richard F. Shaw, Ph.D. candidate, Department of Oceanography, University of Maine at Orono, Ira C. Darling Center, Walpole, ME 04573, pers. commun. May 1980.
[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

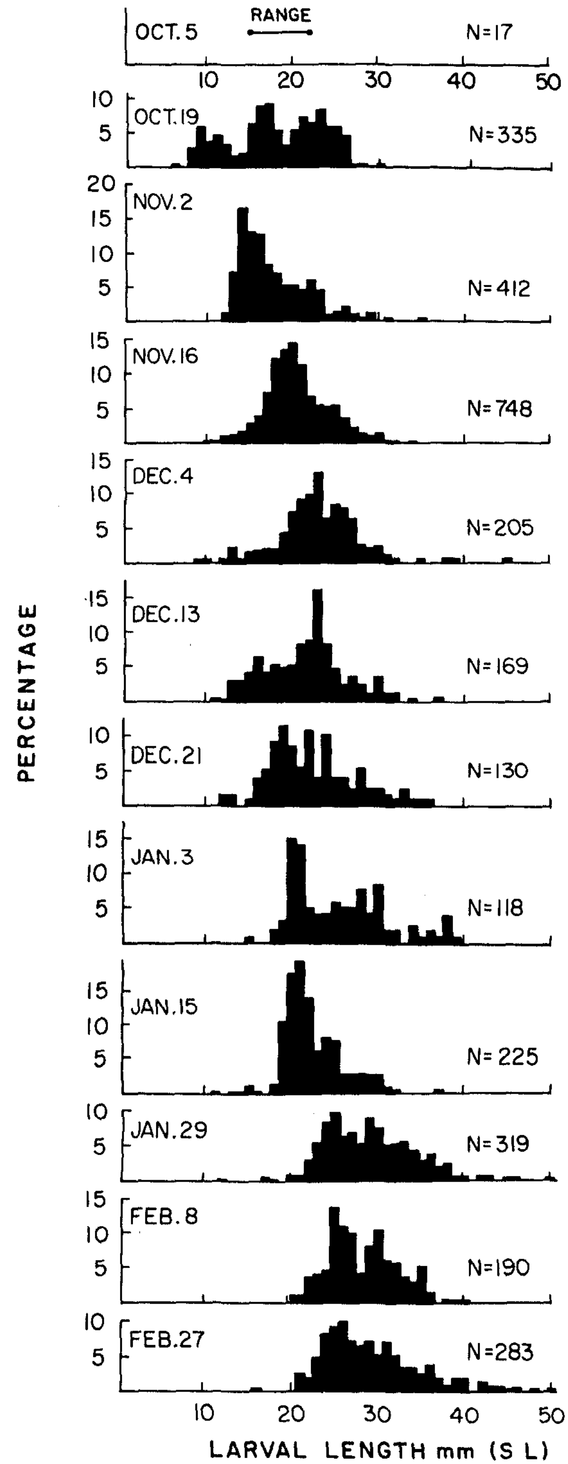

FIGURE 2.—Length-frequencies of Atlantic herring larvae captured at night in the buoyed and anchored nets in the Sheepscot River estuary, Maine, 5 October 1978 to 27 February 1979.

larger larvae from the 19 October population remained. By 16 November there was only one major size mode of larvae in the estuary. During December a second size mode of smaller larvae began to appear and in late December and early January at least two modes were present. By 27 February the two modes were no longer distinguishable. The appearance of the larval group in December was also evidenced by a leveling off of the decline in larval catch rate for that month (Figure 3). The catch rates then increased in January as the second group became established in the estuary.

Assuming the otolith growth increments are deposited with a daily periodicity, increment counts can be used to estimate larval age and growth rates. Figure 4 shows the age structure of the Atlantic herring larvae captured with the towed net in the estuary. The larger and presumably older larvae represented in the 19 October sample of the buoyed and anchored nets (Figure 2) were not detected in the towed net samples; there appeared to be only one major age-group of larvae occupying the estuary through November. The addition of the second age-group of larvae was readily apparent by 10 January and resulted in a shift of the age-frequencies to the reader's right. This second and younger group of larvae was present until the last sampling date (6 March), when the remnant larvae from the first group were detected as a negative skewness in the age-frequency histogram.

The bottom panel of Figure 4 shows the bimodal

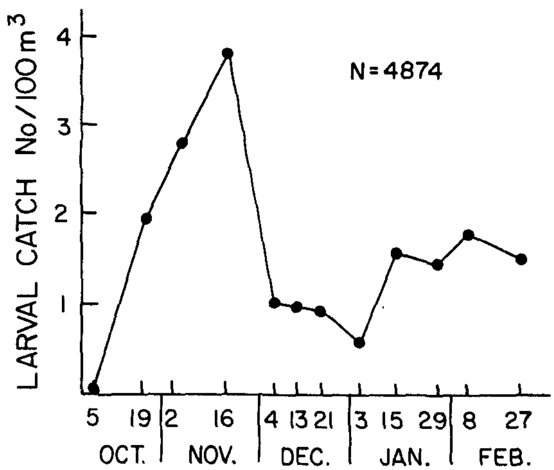

FIGURE 3.—Catch rates of Atlantic herring larvae for the buoyed and anchored nets in the Sheepscot River estuary, Maine, based on flowmeter readings.

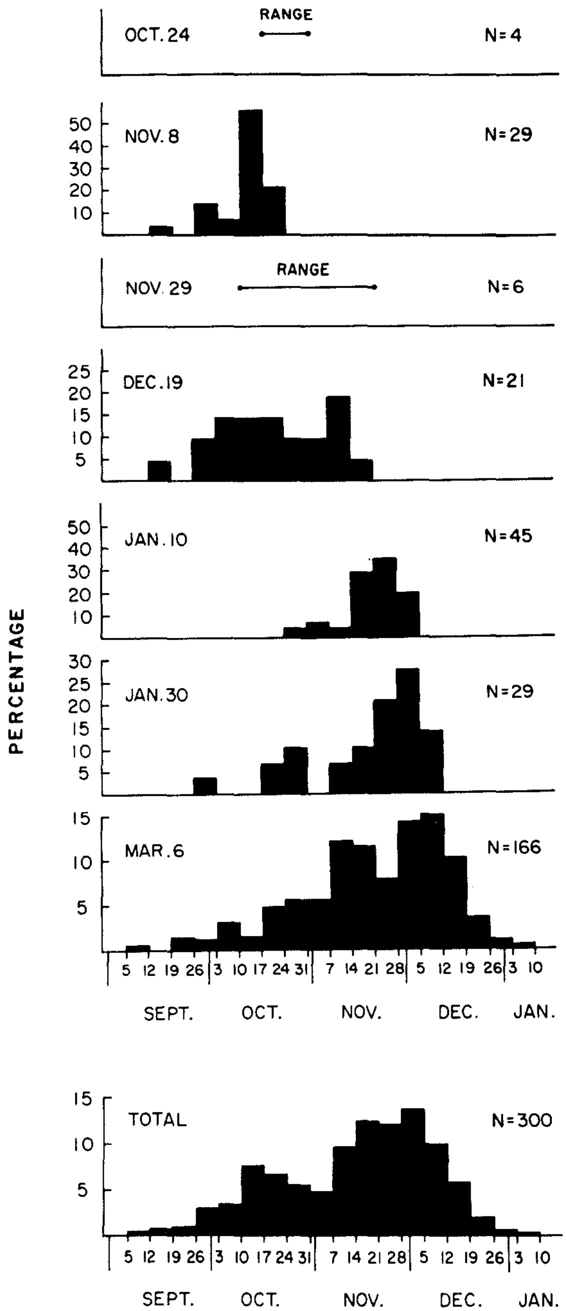

FIGURE 4.—Age distributions of Atlantic herring larvae caught in the towed nets as determined by daily growth increments in the otoliths. The ages are represented as the times of first daily growth increment formation. The distributions for the individual sample dates and the total for all the sample dates are given. The dates on the abscissa correspond to the time of formation of the first otolith daily growth increment. These dates are determined by subtracting the number of days, represented by the number of otolith increments, from the date of capture. Two modes are apparent in the total histogram.

age distribution of larvae from all the towed samples. This bimodal age-frequency distribution was analyzed graphically by the method of Harding (1949) (Figure 5). The total age-frequencies were plotted on probability paper as cumulative percentages, and were found to fall on a sigmoidal curve having a point of inflection on the 32% vertical. The fitted line EF in Figure 5 is the resultant of the two straight lines AB and CD which were found by assuming the data to be bimodally distributed (see Harding 1949 for a more complete discussion). Line AB represents those larvae (about 32% of the total) in which the first otolith growth increment was deposited before 30 October. This date is approximately the point of inflection of the plotted data. Line CD represents the second, younger group of larvae (about 68% of the total). The two straight lines, AB and CD, indicate that the two groups of Atlantic herring larvae which entered the estuary were normally distributed with respect to age. The mean dates on which the first otolith growth increments were laid down for each age-group were determined by the intersection of lines AB and CD with the vertical at 50%. The standard deviations of these dates were estimated from the points where the two lines intersect the verticals at 15.87% and 84.13%, the standard deviation being half this distance on the Y-axis. The mean dates on which the first daily growth increments were laid down were approxi-

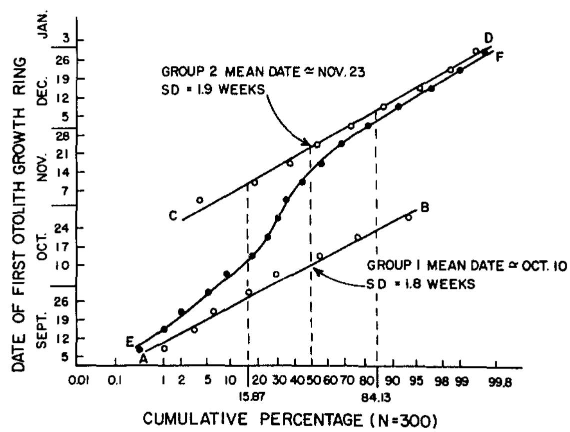

FIGURE 5.—Probability plot of the total bimodal age distribution of Atlantic herring larvae depicted in Figure 4. The dots are the dates on which the first otolith daily growth increment was formed in each larva and are plotted as cumulative percentages. The circles are the cumulative percentages for each of the 2 age-groups using the inflection point of the sigmoidal curve as a dividing point for the two groups. See text for explanation.

mately 10 October for the first group of larvae and 23 November for the second. This analysis indicates, along with the length-frequency data (Figure 2) and the larval catch rates (Figure 3), that there were at least two peaks in spawning effort along the Maine coast, separated by about 6 wk, and that the two groups of larvae entered the estuary at separate times. The times of hatching for each group of larvae can be approximated by assuming that the first otolith daily growth increment is formed at the time of yolk-sac absorption (Rosenberg and Lough footnote 4) and allowing about 5 d for yolk-sac absorption at 10° C (Blaxter and Hempel 1966). The two broods of larvae which entered the estuary in November and December were probably hatched, therefore, in early October and mid-November, and were probably spawned in late September and early November.

Larval Growth Rates

Growth of the larvae was examined separately for each of the two major age-groups which entered the estuary. The first group included those in which the first otolith daily growth increment was laid down before 30 October, which is the dividing point between the two age distributions discussed above. The second group of larvae included those in which the first daily growth increment was laid down on or after 30 October.

Both age-groups of larvae experienced approximately a 2-3 wk period of retarded growth. The changes in growth rate appeared as breaks in the plotted data in Figures 6 and 7. Figure 2 showed also that modal lengths increased only slightly, if at all, from 29 January to 27 February. The first major group of larvae to enter the estuary showed retarded growth (Figure 6) beginning at a length of about 35 mm and about 80-100 d after 10 October, the mean date on which the first otolith daily growth ring was formed (Figure 5). Thus, this period of retarded growth began during the latter half of January and continued until early February. The second major group to enter the estuary showed retarded growth (Figure 7) beginning at a length of about 26 mm, and 50-60 d after 23 November, the mean date of the first otolith daily growth ring for group 2 (Figure 5). This period of retarded growth also began during the latter half of January and continued until early February. It appears, then, that these two groups of larvae, which differed in age by about 6 wk and in length by about 9 mm, experienced similar reductions in their growth rates during the same period in late January and early February. Apparently the environment at this time was not conducive to their growth.

Assuming that growth was interrupted during late January and early February for each of the 2 age-groups of larvae, regression lines were calculated for those larvae caught before the interruption in growth and for those caught after. The larvae caught 30 January were therefore not included (Figures 6, 7). The slopes and elevations of the two regression lines for each age-group were compared using the t-test described by Zar (1974: 228-230). There was no significant difference between slopes for group 1 but the elevations differed significantly ($P < 0.01$). The two regression lines for group 2 differed significantly in slope ($P < 0.05$) and in elevation ($P < 0.01$). Group 1 larvae, then, grew about 2.1 mm/wk before and after the interrupted growth period. Group 2 larvae grew approximately 2.0 mm/wk before this period and about 1.5 mm/wk after.

DISCUSSION

Previous workers have reported polymodal length-frequency distributions of Atlantic herring larvae in the Gulf of Maine-Bay of Fundy areas (Tibbo et al. 1958; Das 1968; Graham et al. 1972; Boyar et al. 1973). Graham et al. (1972) detected two broods of Atlantic herring larvae during September 1964 in the Boothbay area of the western Gulf of Maine, which includes the Sheepscot River estuary. The two broods were indicated by length-frequency modes of 9 and 13 mm. They reported that in 1965 only a single brood was detected in the area initially and that a second group of smaller larvae appeared in November. They suggested that the variations in lengths of the larvae might be attributed to the location of the Boothbay area within a coastal zone of transition in hatching times. Atlantic herring larvae hatch earlier in the eastern coastal Gulf of Maine than in the west, and may be carried westward and into the Boothbay area by coastal currents (Graham 1970; Graham et al. 1972). This may explain the variation in modal sizes on 19 October when the buoyed and anchored nets (Figure 2) captured larvae recently hatched (<10 mm) and others obviously older. The two groups of larvae captured in November and December (Figures 2, 4) perhaps also drifted along the coast before entering the estuary, since each group was about 4 wk old when first sampled.

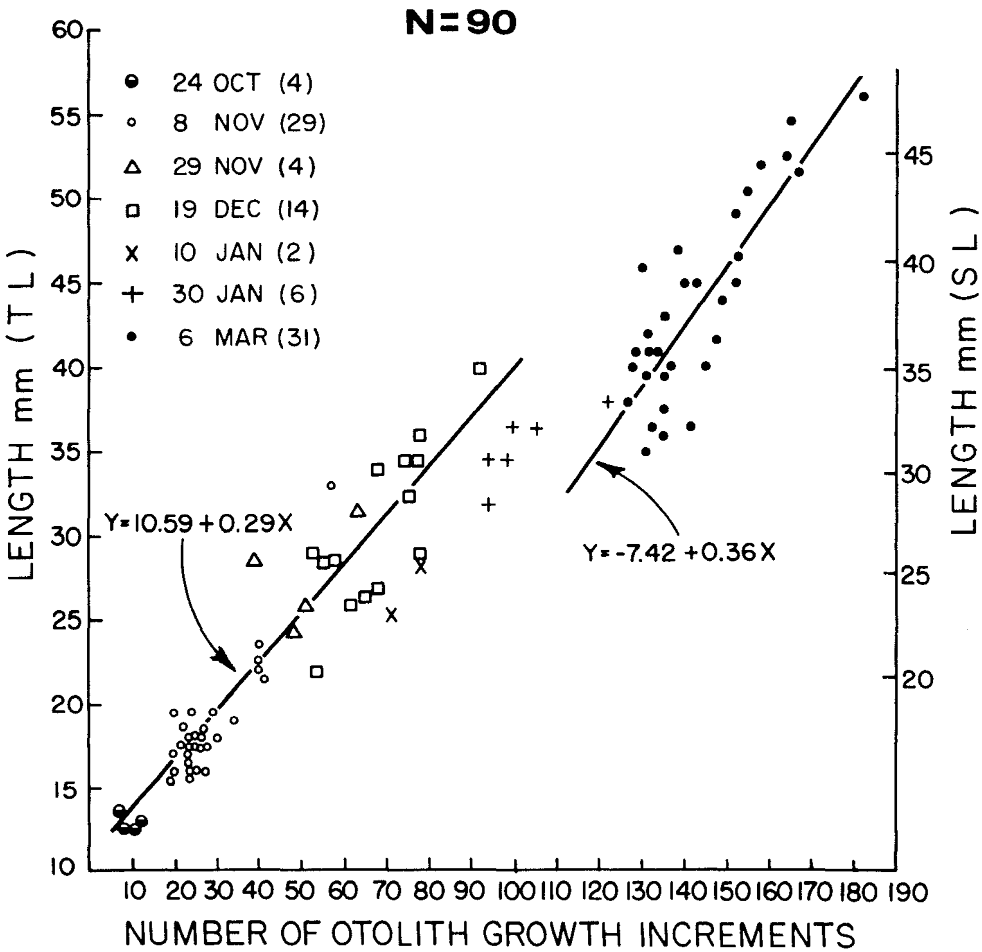

FIGURE 6.—Growth of the first group of Atlantic herring larvae which entered the Sheepscot River estuary, 1978-79. This includes all larvae from the towed net samples in which the first otolith daily growth increment was formed before 30 October. The plotted symbols indicate the collection date and the numbers in parentheses indicate sample size. Regression lines were calculated for the samples collected before and after the winter period of interrupted growth and the 30 January samples were therefore not included.

The growth rates of Atlantic herring larvae in the Sheepscot estuary as determined using daily growth increments in the otoliths were about 2 mm/wk, excluding the winter period of retarded growth. The growth rate of group 2 larvae, however, was lower after this period. Our estimates of larval growth rates, excluding the retarded growth period, are comparable with autumn and spring values reported by other workers (Table 1). Rosenberg and Lough (footnote 4) used daily growth increments in the otoliths to study the growth of Georges Bank herring larvae. The larvae were from a short sampling period (1-18 October 1976), but the authors estimated the growth rate to be about 2.4 mm/wk. This October growth rate estimate is greater than our fall and spring estimates, possibly the result of different water temperatures. The relatively wide range in esti-

TABLE 1.—Published growth rate estimates for fall spawned Atlantic herring larvae in the northwest Atlantic.

Growth rate (mm/wk)	Method used	Period studied	Source
1.7	Mean lengths	First 150 days	Tibbo et al. 1958
<1	Mean lengths	Oct.-June	Sameoto 1971, 1972
1-2	Mean lengths	Nov.-Mar.	Boyar et al. 1973
1.4-1.8	Mean lengths	Sept.-Dec.	Graham et al. 1972
2	Modal lengths	Sept. and Oct.	Das 1968, 1972
<1	Modal lengths	Winter	Das 1968, 1972
1.5	Modal lengths	April	Das 1968, 1972
2	Modal lengths	May	Das 1968, 1972
2.4	Larval otoliths	1-18 Oct.	Rosenberg and Lough 1977

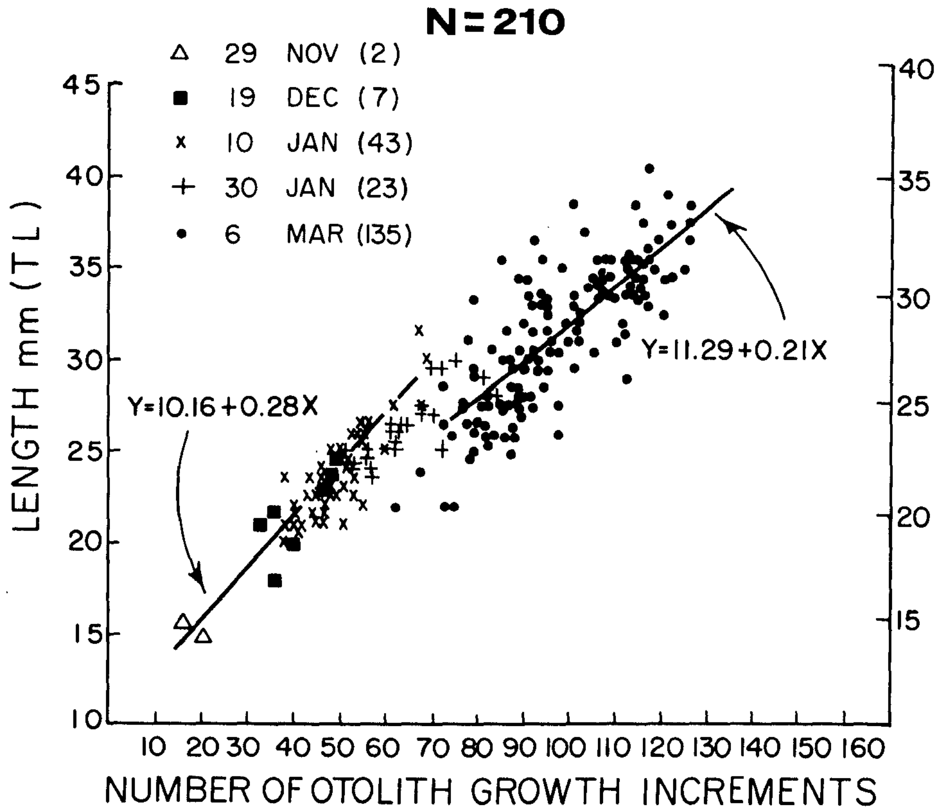

FIGURE 7.—Growth of the second group of Atlantic herring larvae which entered the Sheepscot River estuary, 1978-79. This includes all larvae from the towed net samples in which the first otolith daily growth increment was formed on or after 30 October. The plotted symbols indicate the collection date and the numbers in parentheses indicate sample size. Regression lines were calculated for the samples collected before and after the winter period of interrupted growth and the 30 January samples were therefore not included.

mates reported by others were perhaps developed from samples containing more than 1 age-group. Such combinations are difficult to distinguish in length-frequency data as pointed out by Das (1968, 1972) and Graham et al. (1972). Graham (in press) reported that from one to as many as four broods of larvae entered the Sheepscot estuary annually in recent years.

The winter retardation of larval growth rate observed in the Sheepscot estuary (Figures 6, 7) was more brief than the general slowing down of growth throughout the winter reported by others (Tibbo et al. 1958; Das 1968, 1972; Graham et al. 1972; Boyar et al. 1973). The duration of slowed growth lasted only 2 or 3 wk, from the latter half of January to early February, and occurred approximately when the second group of larvae was abundant in the estuary, but the exact cause of the retarded growth is not clear. Midwinter in general has been shown to be a period of stress for larval herring. Chenoweth (1970) showed that the relative condition of Atlantic herring larvae was poorest in February 1965, 1966, and 1967 and in January 1968 and that these periods of low condition factors coincided with the high mortalities reported by Graham and Davis (1971). Midwinter is a time when food densities are lowest (Sherman and Honey[7]), when water temperatures approach the lethal limit (Graham and Davis 1971) and when the feeding activity of the larvae is lowest (Sherman and Honey 1971). Any or all of these factors may have contributed to the period of retarded growth of larvae in our study.

In conclusion, it appears that the ages of larval herring determined by the otolith growth incre-

[7]Sherman, K., and K. Honey. 1970. Seasonal succession of the food of larval herring in a coastal nursery area. ICNAF Res. Doc. 70/72.

ments are in good agreement with the observed progression of length-frequencies with time, and that such precise age determinations hold much potential for further work on the dynamics of larval fishes. However, it would be advisable to investigate further, under controlled laboratory conditions, the factors controlling the growth of Atlantic herring larvae and otolith growth increment deposition.

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