

AGE AND GROWTH OF LARVAL ATLANTIC HERRING, *CLUPEA HARENGUS* L., IN THE GULF OF MAINE-GEORGES BANK REGION BASED ON OTOLITH GROWTH INCREMENTS

R. GREGORY LOUGH, MICHAEL PENNINGTON, GEORGE R. BOLZ, AND ANDREW A. ROSENBERG¹

ABSTRACT

An estimate of the age and growth of herring larvae over their first 6 months of life is made by examining presumed daily growth increments in their otoliths. A Gompertz growth curve fitted to 311 autumn-spawned specimens collected in the Gulf of Maine-Georges Bank region describes the mean length at age (based on a range of 7-160 otolith increments) from an initial hatching size of 5.7 mm SL to a mean length of 30.9 mm at 175 days. A larva with 7 growth increments is estimated to be on average 25 days old with a mean length of 12.7 mm. Larvae reared in the laboratory at 10°C began initial increment deposition on average 4.5 days from hatching at the time of yolk-sac absorption, and the second increment was deposited an average of 12 days from hatching. The rearing experiments were terminated before an increment-day relation could be established, but the third increment was estimated to be formed on average 22 days from hatching. Support for the assumption that increment deposition becomes daily at least after the third increment is made by two independent methods. Based on the fitted Gompertz curve, average growth rates for herring larvae increased from 0.25 mm/day at hatch to 0.30 mm/day at 20 days and declined to <0.15 mm/day after 75 days of age during the winter period. This agrees closely with estimated field rates.

Atlantic herring, *Clupea harengus* L., spawn demersal eggs during late summer-autumn on the shoaler (<40 m bottom depth) regions of Georges Bank and around the perimeter of the Gulf of Maine (Bigelow and Schroeder 1953; Boyer et al. 1973; Lough and Bolz 1979²). Hatching occurs after 8-9 d at 10°C (Cooper et al.³), and shortly thereafter the larvae are dispersed throughout the water column by the vigorous tidal stirring characteristic of this region (Bumpus 1976). By following length-frequency means or modes between successive surveys, average larval growth rates have been estimated on field populations of larvae in the Gulf of Maine-Georges Bank region by Tibbo et al. (1958), Tibbo and Legaré (1960), Das (1968, 1972), Graham et al. (1972), Sameoto (1972), Boyar et al. (1973), Lough et al. (1979),⁴

and others. Larval herring grow at an overall average rate of about 5 mm/mo (0.2 mm/d) from hatch (6 mm SL) to metamorphosis in the spring. Metamorphosis is a gradual transition to adult characteristics generally achieved by the time the fish are 50-55 mm, but some studies report metamorphosis occurring at much smaller lengths of 30-35 mm (Blaxter and Staines 1971; Boyar et al. 1973; Ehrlich et al. 1976; Doyle 1977).

Knowledge of larval herring growth is an important component in the estimation of age-specific mortality rates, which can be used to study variations in larval survival in relation to size of succeeding year classes. However, field estimates of larval growth only provide average rates of growth so that their use in comparative studies is limited by the sometimes polymodal length frequencies and subjective nature of connecting corresponding length modes. With the development of accurate growth models, populations can be compared by region and season with various environmental factors which may be affecting growth and hence survival of larvae. Techniques are now available for the accurate aging of larval and juvenile fishes based on

Clupea harengus L.) larvae in relation to environmental factors, spawning stock size, and recruitment for the Georges Bank area, 1968-1977 seasons. ICNAF Res. Doc. 79/VI/112, 47 p.

¹Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

²Lough, R. G., and G. R. Bolz. 1979. A description of the sampling methods, and larval herring (*Clupea harengus* L.) data for surveys conducted from 1968-1978 in the Georges Bank and Gulf of Maine areas. Northeast Fisheries Center, Natl. Mar. Fish. Serv., NOAA, Woods Hole Lab. Ref. 79-06, 230 p.

³Cooper, R. A., J. R. Uzmann, R. A. Clifford, and K. J. Pecci. 1975. Direct observations of herring (*Clupea harengus* L.) egg beds on Jeffreys Ledge, Gulf of Maine in 1974. ICNAF Res. Doc. 75/93, 6 p.

⁴Lough, R. G., G. R. Bolz, M. D. Grosslein, and D. C. Potter. 1979. Abundance and survival of sea herring (*Clupea haren-*

growth increments or lamellae in their otoliths, thus providing a detailed chronological record of events in the growth history of an individual fish (Pannella 1971, 1974; Scott 1973; Brothers et al. 1976; Struhsaker and Uchiyama 1976; Ralston 1976; Taubert and Coble 1977; Barkman 1978; Methot and Kramer 1979; Radtke 1980⁵; Radtke and Waiwood 1980; Steffensen 1980; Wilson and Larkin 1980; Uchiyama and Struhsaker 1981; Barkman et al. 1981; Brothers 1981; Brothers and McFarland 1981; Methot 1981). Evidence for the presence of apparent daily otolith growth increments in larval herring collected along western Gulf of Maine in October 1976 was given in a preliminary report by Rosenberg and Lough.⁶ Further work by Lough et al.⁷ led to the development of a growth model extending through the autumn-winter period. Townsend and Graham (1981) recently used otolith aging techniques to examine the age structure of larval herring entering the Sheepscot River, Maine, estuary during autumn-winter 1978-79.

The objective of this study is to summarize our findings on the age and growth of larval herring otoliths during the first 6 mo of life, from hatching to a length of ca. 31 mm, based on larvae reared in the laboratory and collected in the Gulf of Maine-Georges Bank region. Also, a Gompertz growth curve is fitted to the length-at-age data based on "daily" growth increment in their otoliths to describe the shape of the average larval herring growth curve in this region from October through March 1976-77. The present study was initiated by the International Commission for the Northwest Atlantic Fisheries (ICNAF) (Lough et al. 1981) and the U.S. participation was conducted concurrently as part of the MARMAP (Marine Resources Monitoring, Assessment, and Prediction) program of the Northeast Fisheries Center, which measures long-term changes in the variability of fish stock abundance off the northeast coast of the United States (Sherman 1980).

METHODS

Larval herring for otolith studies were collected at selected stations within a standard grid

⁵Radtke, R. L. 1980. The formation and growth of otoliths from redfish (*Sebastes* spp.) larvae from the Flemish Cap (Division 3M). NAFO SCR Doc. 80/IX/153, 6 p.

⁶Rosenberg, A. S., and R. G. Lough. 1977. A preliminary report on the age and growth of larval herring (*Clupea harengus*) from daily growth increments in otoliths. ICES C.M. 1977/L:22, 15 p.

of sampling stations covering the western Gulf of Maine, Georges Bank, and Nantucket Shoals areas on five ICNAF larval herring surveys conducted from October 1976 through March 1977 (Table 1, Fig. 1). Larvae normally were collected at stations where high densities were encountered. Standard ICNAF double-oblique continuous hauls (61 cm bongo net, 0.505 and 0.333 mm mesh nets) were made at each station to a maximum depth of 100 m, or to within 5 m of the bottom in shoaler areas, while the vessel was underway at 3.5 kn. A standard haul ranges in duration from 5 to 25 min; each bongo net filtering between 100 and 1,000 m³ of water depending on the duration (maximum depth) of the haul. Further details of the sampling gear and protocols can be found in Lough and Bolz (footnote 2). Immediately after the nets were brought aboard the vessel, larvae were sorted from the untreated 0.505 mm mesh plankton sample and frozen in dishes. Extra hauls occasionally were made to collect sufficient numbers of larvae. Tempera-

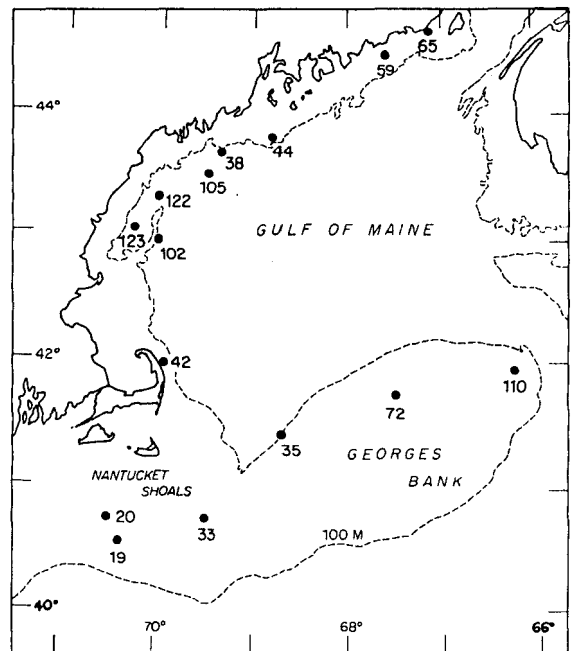


FIGURE 1.—Station locations in the Gulf of Maine-Georges Bank region where larval herring were collected for otolith aging over the 1976 spawning season.

⁷Lough, R. G., M. R. Pennington, G. R. Bolz, and A. S. Rosenberg. 1980. A growth model for larval sea herring (*Clupea harengus* L.) in the Georges Bank-Gulf of Maine area based on otolith growth increments. ICES C.M. 1980/H:65, 22 p.

TABLE 1.—Station information for larval herring specimens collected for otolith analysis by 61 cm bongo net (0.505 mm mesh) oblique hauls from autumn 1976 through winter-early spring 1977 in the Gulf of Maine-Georges Bank region.

Vessel	Cruise no.	Station	Lat. N	Long. W	Area	Date (GMT)	Time (GMT) (Night or Day)	Bottom depth (m)	Temp. (°C) at 20 m	No. larvae	Mean standard length (mm) ¹	Mean no. otolith increments ¹
<i>Annandale</i>	76-01	38	43°37'	69°22'	W. Gulf of Maine	8 Oct. 1976	0300 (N)	114	12.9	35	15.5 (2.7)	19.3 (6.0)
		44	43°44'	68°50'		8 Oct.	1415 (D)	76	13.0	39	14.3 (1.7)	16.0 (4.0)
		59	44°25'	67°35'		9 Oct.	1515 (D)	57	13.0	9	17.1 (2.3)	22.8 (9.3)
<i>Wieczno</i>	76-03	65	44°36'	67°07'	Georges Bank	13 Oct.	0330 (N)	85	12.7	37	17.5 (3.2)	23.2 (9.8)
		72	41°45'	67°30'		28 Oct.	0650 (N)	42	2 ¹ 3.8	18	14.9 (1.7)	12.1 (3.5)
		42	41°54'	69°50'		1 Dec.	0002 (N)	60	8.0	9	17.8 (2.4)	27.8 (10.0)
<i>Researcher</i>	76-01	35	41°21'	68°42'	Georges Bank	1 Dec.	0626 (N)	108	8.6	3	21.1 (0.8)	41.7 (5.9)
		102	42°58'	70°00'		8 Dec.	1030 (N)	100	7.4	29	18.0 (1.6)	22.6 (7.9)
		105	43°30'	69°30'		9 Dec.	1100 (N)	150	7.5	12	18.2 (1.3)	24.4 (8.1)
<i>Mt. Mitchell</i>	77-01	110	41°51'	66°15'	Georges Bank	11 Dec.	0955 (N)	80	8.4	37	21.3 (2.0)	44.4 (8.1)
		19	40°33'	70°20'		15 Feb. 1977	0701 (N)	66	0.6	26	29.9 (2.2)	109.2 (19.0)
		20	40°45'	70°30'		15 Feb.	1026 (N)	65	0.0	2	26.7 (1.4)	87.0 (2.8)
<i>Anton Dohrn</i>	77-01	122	43°14'	70°01'	W. Gulf of Maine	24 Feb.	1620 (D)	124	3.5	10	26.0 (0.7)	114.6 (15.6)
		123	43°00'	70°15'		24 Feb.	1933 (D)	166	3.0	10	28.1 (2.3)	122.1 (12.8)
		33	40°45'	69°30'		17 Mar.	2230 (D)	47	2 ¹ 4.3	34	30.2 (2.4)	129.4 (14.0)

¹Number within parentheses is 1 standard deviation.

²Only surface temperature available.

ture data at each station were obtained from expendable bathythermograph traces or surface bucket readings.

Larvae were reared from fertilized eggs in the laboratory in order to determine the age at which increment deposition first begins in larval herring otoliths. A batch of herring eggs, stripped from several ripe and running adults collected along the western Gulf of Maine near Jeffreys Ledge, was fertilized on 17 October 1978 and reared at the NMFS Narragansett Laboratory at 10°C by G. Laurence for use in various feeding experiments. Larvae were maintained in special rearing aquaria described by Beyer and Laurence (1981) with a photoperiod of 12 h light and 12 h dark and fed wild plankton at high densities (>3 plankters/ml). Approximately 15 larvae were removed from the rearing aquaria daily from hatching on 28 October through 15 November and preserved in 75% ethyl alcohol.

Prior to removing the otoliths, larvae were staged according to Doyle (1977) and measured for standard length (snout to caudal peduncle) and head length (snout to sagitta in normal position) to the nearest 0.1 mm. The largest otoliths (sagittae) were removed from both sides of the head when possible and mounted in Canada balsam or Permunt.⁸ The otoliths were whole mounted and little difficulty was found in reading them intact so that further preparation was unnecessary. The 2-sagittae and 2-astericae obtained per individual from the laboratory-reared larvae were virtually impossible to distinguish at this early stage; however, the number of growth increments was identical for both sets of otoliths from the same individual.

The otoliths were viewed by transmitted light and growth increments were counted using a Zeiss compound microscope-video system with a magnification range of 630× for the largest otoliths and 1000× or 2000× for the smallest. Differential interference microscopy was particularly helpful in distinguishing increments of the smallest otoliths. The resolving power of our microscope is in the range of 0.2-0.5 μm. A minimum of three counts was made on all otoliths or counts were repeated until a mean value was reached with a maximum acceptable range of 5% variability. Routine otolith measurements made to the nearest micron as illustrated in Figure 2 included the following: 1) anterior-posterior di-

⁸Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

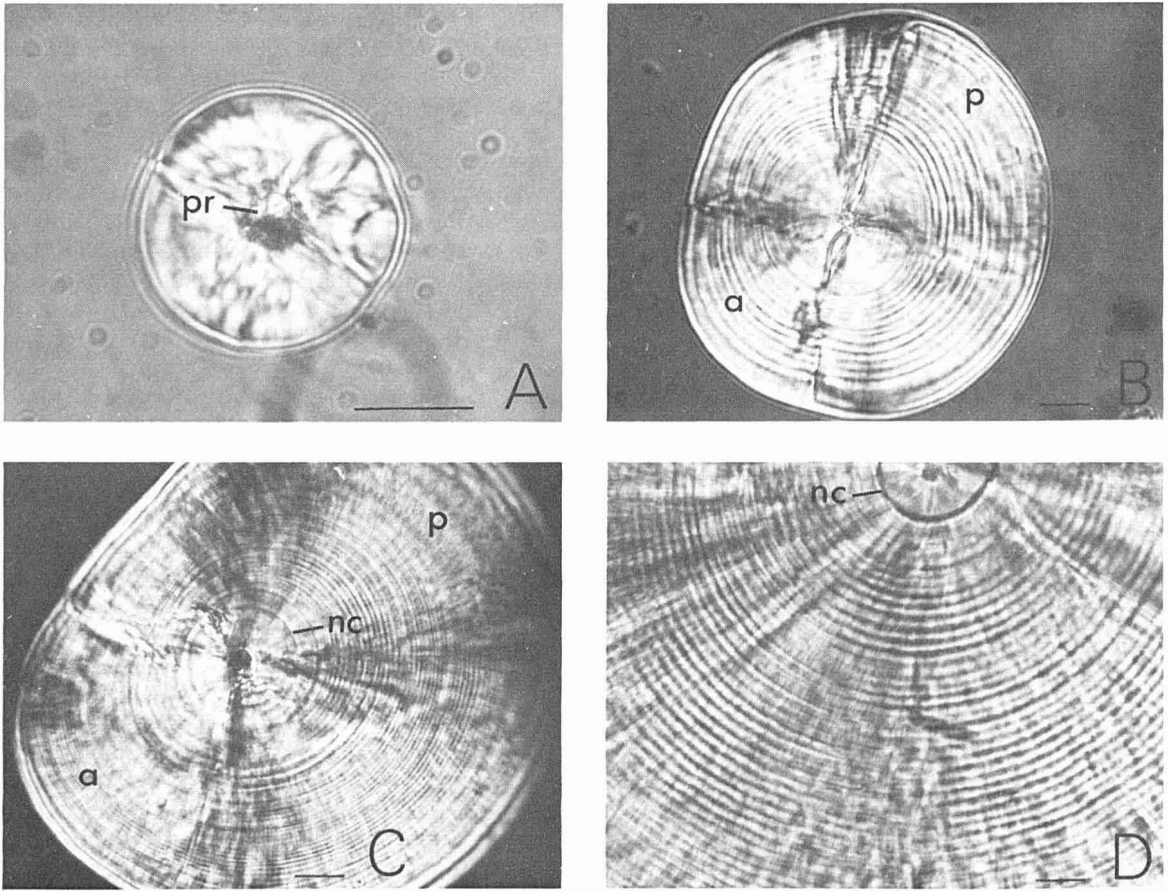


FIGURE 2.—Sagittae of herring larvae, *Clupea harengus*. Bar on photographs represents $10\ \mu\text{m}$; pr = primordium, a = anterior, p = posterior, nc = nuclear check. A. Otolith from laboratory-reared larva, 8.4 mm SL, showing 2 growth increments ($1000\times$). Additional increments are optical artifacts. B. Otolith with 23 increments showing band of thin, poorly defined 4-5 increments around nucleus; 18.6 mm SL; *Ammandale* 76-01, Stn. 38. C. Otolith with 51 increments ($630\times$). Note the first 3-4 thin, poorly defined increments immediately surrounding nuclear check; 19.9 mm SL; *Researcher* 76-01, Stn. 105. D. Otolith with 54 increments ($630\times$), posterior view. Note pattern of increment thickness from initial thin, poorly defined 7-9 increments encircling a heavy nuclear check increasing to maximum thickness at 10th-35th increments and then decreasing thickness towards the edge; 21.6 mm SL; *Researcher* 76-01, Stn. 35.

ameter (otolith length); 2) lateral diameter: a line perpendicular to anterior-posterior axis; 3) nucleus diameter: whole otolith at hatching without increments or to inner edge of first increment; 4) anterior radius: nucleus center (primordium) to anterior edge; and 5) posterior radius: nucleus center (primordium) to posterior edge. Selected otoliths were photographed, enlargements made, and increment thicknesses were measured across a posterior radius from the nucleus using a Zeiss MOP Digital Image Analyzer System.

All field-collected larvae used in this study for otolith aging were frozen, whereas the labora-

tory-reared larvae were preserved in 75% ethyl alcohol, and larvae referred to in other corroborative field studies were preserved in Formalin. Theilacker (1980) reported that the amount of shrinkage of northern anchovy larvae, *Engraulis mordax*, varies with fish size and duration of time larvae are retained within the net. Larvae smaller than 11 mm SL net-treated for 20 min prior to preservation. We estimate that nearly all herring larvae collected on ICNAF surveys have been dead at least 20 min prior to preservation. An additional 3% shrinkage due to 5% Formalin preservation was recommended by Theilacker

for all body parts after net-treatment, whereas preservation in ethyl alcohol (80%) did not cause any additional shrinkage in standard length. Townsend and Graham (1981) indicated that frozen herring larvae (27-45 mm TL) may shrink 3-4% more than Formalin-preserved larvae. From our experience we find that length measurements of frozen larvae can be more variable than those of Formalin-preserved larvae; however, a thorough study has not been made. No correction factor was applied to our field-collected frozen larvae because of the uncertainty of time prior to preservation and the effect of freezing on shrinkage. We do not feel that the Gompertz population growth curve fit to the uncorrected field-collected larvae would be significantly altered with respect to shape compared with corrected data. When a direct comparison is made in this paper between laboratory-reared and field-estimated larval lengths, a shrinkage correction factor applied to the lab data will be specified based on Theilacker's (1980) work which probably is adequate for all clupeidlike larvae.

RESULTS

Otoliths from 311 herring larvae caught in plankton hauls were processed in this study covering their first 6 mo of life from October through March 1977 (Table 1, Fig. 1). Approximately 58% of the larvae were collected along the western Gulf of Maine, 23% from Nantucket Shoals, and 19% from Georges Bank. ICNAF surveys have never been conducted during the month of January so that there is a gap in time in our collection of larval otolith data from mid-December 1976 to mid-February 1977. The field-collected larvae ranged in length from 11 to 35 mm with most of the western Gulf of Maine larvae falling into the 11-31 mm size range; the Georges Bank larvae, 19-25 mm; and the Nantucket Shoals larvae, 26-35 mm. The number of otolith increments counted from the field-collected larvae ranged from 7 to 160. Since we were not able to collect any recently hatched larvae <11 mm length for otoliths on these surveys, laboratory-reared larvae had to suffice for the smallest size.

Laboratory-Reared Larvae

Hatching of the laboratory-reared larvae occurred over a 5-d period with 50% hatch estimated on 28 October 1978 for a mean incubation

of 11 d. Yolk-sac resorption was estimated to be 50% complete 4-5 d after hatching, and 99% complete 6 d after hatching. The larvae began actively feeding at yolk-sac resorption and appeared to be healthy without any abnormalities throughout the more than 3 wk of rearing. Mortality over the first 13 d from hatching averaged 12%/d which is considered low. The age of larvae from hatching midpoint with 0-3 increments is given in Table 2 and Figure 3. The first increment appeared on larval otoliths that ranged in age from 0 to 9 d from hatch with a middate of 4.5 d which indicates that the first increment is deposited near the end of yolk-sac resorption. Larvae staged according to Doyle (1977) showed a progression of the three substages 1a-1c over the first 3 d from hatch so that after the third day only remnants of yolk sac remained.

The second growth increment occurred in larvae 6-18+ d old with a middate of 12 d from hatch or 7.5 d from the middate of the first increment formation. The third increment was observed for the first time on a larva 16 d from hatch, but unfortunately sampling was terminated before the

TABLE 2.—Distribution of otolith growth increments, age in days from hatching midpoint, and mean standard length of herring larvae reared in the laboratory at 10°C.

Increments	Age (d)		Mean standard length (mm) ¹	No. larvae
	Midpoint	Range		
0	3	0-6	8.0	8
1	4.5	0-9	8.1	25
2	12	6-18+	9.1	21
3	(22 est.)	16-	9.5	3

¹Measurements made on larvae preserved in 75% ethyl alcohol. Unpreserved mean length of 55 larvae at hatch was 7.66 mm, standard deviation of 0.58 (Beyer and Laurence 1981).

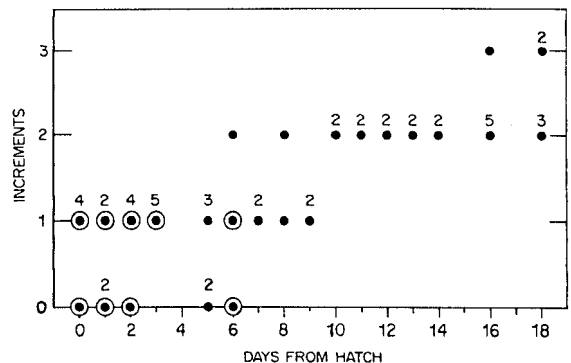


FIGURE 3.—Otolith increment deposition for herring larvae sampled from 50% hatch through 18 d of rearing in the laboratory at 10°C. Encircled points represent yolk-sac larvae. Numbers above points denote numbers of larvae >1.

complete age distribution of 3-increment larvae could be determined. If the range of ages of 3-increment larvae is similar to the 2-increment larvae, then the estimated age of 3-increment larvae would range from 16 to 28 d with a mid-date of 22 d from hatch.

Otolith Growth

The growth and morphology of young herring otoliths has been described previously by Hempel (1959) for specimens ranging in length (total) from 25 to 130 mm collected in the German Bight, by Watson (1964) for Maine herring of 85-285 mm TL, and by Messieh (1975) for Bay of Fundy herring of 32-118 mm TL. Here we describe the growth and morphology of herring otoliths (sagitta) in relation to head length for Gulf of Maine-Georges Bank larvae ranging in size from 5.7 mm (hatching) to 35 mm SL (prior to metamorphosis).

The shape of the larval herring otolith at hatching is essentially spherical having a slight convex distal side and a flat proximal side with three or four furrows radiating from a distinctive central core called a primordium (see Fig. 2). A slight protuberance is apparent on the anterior edge of the otolith from larvae starting at about 20 mm SL which develops into the adult rostrum. With further elongation along the anterior-posterior axis, the otoliths become generally pear-shaped at metamorphosis (45 mm TL) and attain the typical shape of adult herring otoliths by 75 mm (Messieh 1975). The mean diameter of the nucleus, defined here as the size of the otolith at hatching prior to increment deposition, is $22.5 \mu\text{m}$ ($1.1 \mu\text{m}$ SD) based on the laboratory-reared larvae. The otolith increases exponentially in length (anterior-posterior axis) to a mean size of $456 \mu\text{m}$ at 35 mm SL based on the composite field data. Successive dark and light layers are deposited around the nucleus as the otolith grows. A single growth increment comprised of a dark plus light band is generally presumed to represent 1 d. The otolith nucleus of the field-caught larvae is readily discernible as its margin is usually darkened to form a nuclear check (see Fig. 2). In some otoliths an additional increment was seen inside of the check. Messieh and Moore⁹ also have observed 1 or 2, and sometimes up to 5, faint increments inside the nuclear

check of otoliths from herring larvae collected in the Gulf of St. Lawrence. However, no nuclear check was evident in otoliths of the laboratory-reared larvae and no increments were observed within the defined nucleus. Nuclear diameters of the field-caught larvae all fell within the 95% confidence limit of the mean nuclear diameter determined from the laboratory-reared larvae. Immediately surrounding the nucleus of the field-caught larvae, the first 3-9 growth increments appear to be less well defined than succeeding increments, i.e., lower optical density and thinner in width. Distinctive, darker than normal growth layers were noted across an otolith transect but they did not suggest any pattern or complex periodicity as observed by Pannella (1971), nor was there any evidence of subdaily rings as observed for some species by Taubert and Coble (1977), Brothers (1981), and Brothers and McFarland (1981). Scanning electron microscopy techniques will be necessary to resolve the presence or absence of faint increments.

The thickness of successive growth increments was measured on otoliths from three field-caught larvae along a posterior radius starting from the nucleus edge (Fig. 4). Measurements were made only through the penultimate increment in each case as the marginal increment was still in the process of formation and could not always be read clearly. Increment thickness ranged from about 0.6 to $2.4 \mu\text{m}$ along the radii. All three otoliths show the same general pattern of increment thickness up to about 23 increments where the first 7-10 increments are relatively thin ($0.8-1.5 \mu\text{m}$) and increase to near maximum thickness ($2.3 \mu\text{m}$) by about 75 increments. The thickness of the first 3 increments from the laboratory-reared larvae was consistently $0.8-1.0 \mu\text{m}$, which compares closely with the initial increment thickness of the field-caught larvae. Otolith B tends to suggest a prolonged period of relatively thick increments before thinner ones start to be formed, whereas otolith C appears to form thin increments immediately after maximum increment thickness at around 15 increments. The form of the otolith growth curves can be seen more readily in Figure 5 where otolith radii are plotted against the number of increments for the three larvae. These curves suggest that otolith growth is initially slow, increases

⁹S. N. Messieh and D. S. Moore, Marine Fish Division, Fisheries and Oceans, Bedford Institute of Oceanography, Dart-

mouth, N.S., Canada, B2Y 4A2, pers. commun. August-September 1981.

FIGURE 4.—Change in increment thickness for three field-collected herring larvae. Measurements were made along a posterior radius from nucleus edge through the penultimate increment. A. Total of 23 increments (see Fig. 2B); 18.6 mm SL larva; *Annadale* 76-01, Stn. 38. B. Total of 54 increments (see Fig. 2D); 21.6 mm SL larvae; *Researcher* 76-01, Stn. 35. C. Total of 150 increments, only initial 80 measured; 31.0 mm SL larva; *Anton Dohrn* 77-01, Stn. 33.

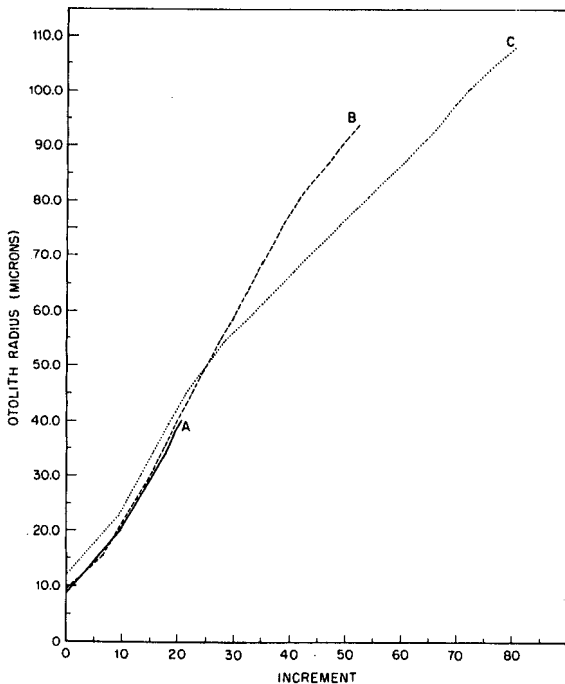
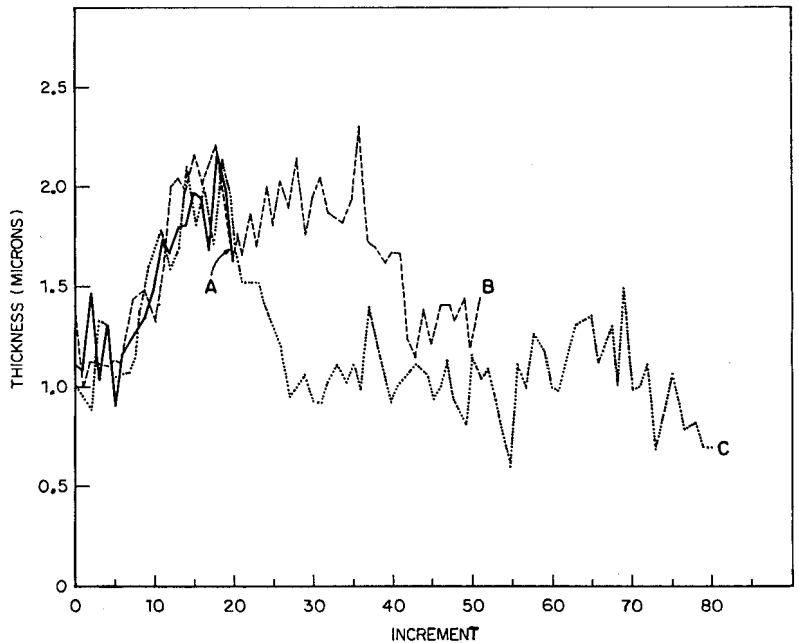


FIGURE 5.—Otolith radii vs. number of increments for the same three larvae in Figure 4.

rapidly, and then levels off at some point. This same general pattern of otolith microstructure was observed by *Brothers and McFarland (1981)* for French grunts.

Various allometric relations were examined between otolith size and growth of the field-caught larvae, and a few are presented here to show the homogeneity of the measurements from the three spawning populations sampled: western Gulf of Maine, Georges Bank, and Nantucket Shoals. A plot of the otolith anterior vs. posterior radii in Figure 6 shows a linear relationship. The posterior radius becomes increasingly longer than the anterior radius with increment deposition. Otolith length plotted against head length

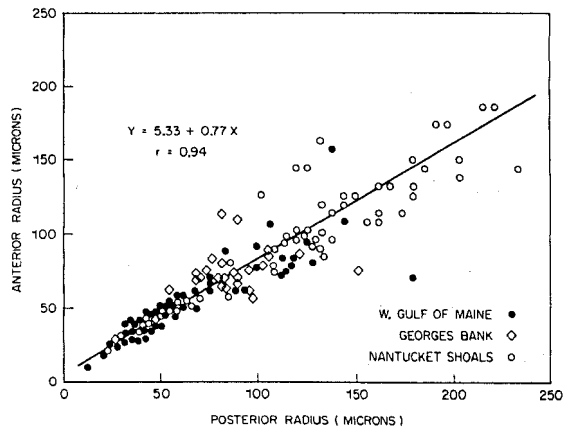


FIGURE 6.—Otolith anterior-posterior relation for herring larvae collected from the three areas: western Gulf of Maine, Georges Bank, and Nantucket Shoals, with composite regression line and correlation coefficient (r).

in Figure 7 also can be expressed by a simple linear relationship. The long axis of the otolith shows a positive allometry with respect to head length for recently hatched larvae to a size of about 35 mm SL. Hempel (1959) reported nearly isometric growth between head and otolith length after metamorphosis for German Bight herring.

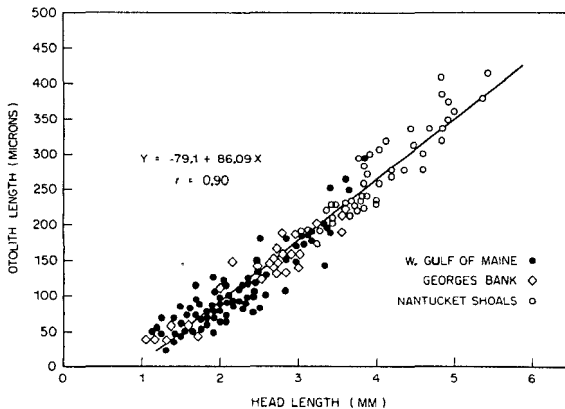


FIGURE 7.—Otolith length (anterior + posterior radii)-head length relation for herring larvae collected from the three areas: western Gulf of Maine, Georges Bank, and Nantucket Shoals, with composite regression line and correlation coefficient (r).

Larval Growth

A composite plot of larval length versus number of otolith increments is presented in Figure 8. A Gompertz growth curve was fitted to the field data to produce a description of the mean growth of larval herring based on the 311 specimens with otolith growth increments ranging from 7 to 160. The Gompertz-type curve (Laird 1969) has been used to describe growth of a wide variety of organisms that often grow exponentially at a rate which is decaying exponentially. Previous use of the Gompertz model to more accurately describe the growth of young fish has been made by Kramer and Zweifel (1970), Sakagawa and Kimura (1976), Zweifel and Lasker (1976), and Methot and Kramer (1979). Using the field data as a starting point, it was assumed that increments were deposited daily at least after the 7th increment so that the equation

$$L = L_7 \exp[k(1 - \exp[-\alpha(r - 7)])], \quad r \geq 7,$$

was taken to represent mean larval length as a

function of age where r , the number of increments, represents age plus some unknown constant (see Pennington 1979 for details of the model fit).

The fitted equation was found to be

$$L = 12.70 \exp[0.89(1 - \exp[-0.03(r - 7)])] \quad \text{for } r \geq 7, \quad (1)$$

where $12.70 = L_7$, the mean length of a 7-increment larvae.

Equation (1) may be rewritten as

$$L = 30.90 \exp[-1.07 \exp(-0.03 r)], \quad r \geq 7, \quad (2)$$

where $30.90 = \hat{L}_\infty$, the asymptotic limit of mean growth during the October-March period. Assuming: 1) for at least $r \geq 7$, increments are deposited daily and 2) a curve in the form of Equation (2) approximates growth from hatch, then denoting age by x ,

$$x = r + c, \quad r \geq 7,$$

from 1), where c is an unknown constant, or

$$r = x - c, \quad x \geq c + 7.$$

Thus

$$L = 30.90 \exp(-1.07 \exp[-0.03(x - c)]), \quad x \geq c + 7, \quad (3)$$

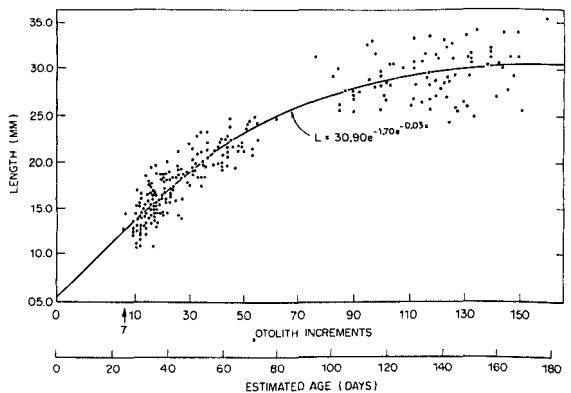


FIGURE 8.—Composite standard length-otolith increment plot for field-collected herring larvae in the Gulf of Maine-Georges Bank region, October 1976-March 1977. A Gompertz curve is fitted to larval length at estimated age, x , over their first 6 mo of life from a mean hatch length of 5.7 mm to an asymptotic limit of mean growth of 30.9 mm. A larva with 7 otolith increments is estimated to be on average 24.8 d old. See text for details.

which, if assumption 2) is reasonable, Equation (3) holds for $x \geq 0$. Letting L_0 denote mean length at hatch ($x = 0$), then solving Equation (3) for c yields,

$$c = \frac{\text{Ln}(3.431 - \text{Ln } L_0) - 0.065}{0.026}$$

Table 3 gives an estimate of the age of larvae with 7 increments (24.8 d) derived from the mean length of recently hatched larvae collected on the Jeffreys Ledge spawning beds (Cooper et al. footnote 3).

When the mean hatching size (L_0) = 5.7 mm, $c = 17.8$ d, and from Equation (3), length as a function of age is given by

$$L = 30.90 \exp[-1.70 \exp(-0.03 x)], \quad x \geq 0. \quad (4)$$

From Equation (4) the mean length at age along with 95% confidence limits, and growth rate (millimeters/day) are estimated from the time of hatch through 175 d in Table 4. Also, the fitted growth curve is shown in Figure 8 with the estimated larval age referenced to the lower scale. The growth curve is based on data with more than 6 increments and a mean length of 5.7 mm at hatch. Obviously, if the functional form changes between age 0 and the age corresponding to 7 increments, then the predicted age of fish with 7 or more increments is biased.

This growth curve is based on larvae that survived to the age when caught. Therefore, the back-casted curve represents the mean length of larvae for a given age which survive and hence, may be higher than the mean length of the total population.

The mean lengths at age of laboratory-reared larvae having 1 and 2 increments from Table 2 fall reasonably close to the extrapolated curve near the origin. The mean length of the laboratory-reared larvae at hatch was reported by Beyer and Laurence (1981) to be 7.66 mm (SD = 0.58 mm). After correcting for a 20-min net-treatment and Formalin preservation shrinkage factor to compare with the field data, their reported mean hatching size is estimated to be 6.4 mm, which is not significantly different from the Jeffreys Ledge diver-collected, Formalin-preserved yolk-sac larvae of 5.7 mm mean SL.

An estimate of $\sqrt{\text{var}(x|r)}$, the standard deviation of age for a fixed number of increments, was made from the field data by Pennington (1979), and its value of 2.9 d compares closely with the

TABLE 3.—Age of larval herring with 7 otolith growth increments estimated from an initial mean hatching size of 5.7 mm (0.54 mm SD) and 95% confidence intervals of the mean. Standard lengths of 100 newly hatched yolk-sac larvae (Formalin¹ preserved) were measured from egg bed samples collected by divers² on the Jeffreys Ledge study site (38 m depth), 8 October 1974.

Hatch length (L_0) (mm)	95% confidence intervals		Estimated age of larva with 7 increments (d)	95% confidence intervals	
	lower	upper		lower	upper
5.7	5.6	5.8	24.8	24.4	25.2

¹Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

²Northeast Fisheries Center's Manned Undersea Research and Technology (MURT) Dive Team.

TABLE 4.—Mean standard length at age, 95% confidence limits, and growth rate (mm/d) of larval herring from hatch through 175 d estimated from the Gompertz growth model fit.

Age (d)	Mean length (mm)	95% confidence limits		Growth rate (mm/d)
		lower	upper	
0	5.7	5.4	6.0	0.25
1	5.9	5.6	6.2	0.26
2	6.2	5.9	6.5	0.26
3	6.4	6.2	6.7	0.26
4	6.7	6.4	7.0	0.27
5	7.0	6.7	7.3	0.27
6	7.2	6.9	7.5	0.27
7	7.5	7.2	7.8	0.28
8	7.8	7.5	8.1	0.28
9	8.1	7.8	8.4	0.28
10	8.4	8.1	8.7	0.29
20	11.3	11.0	11.6	0.30
30	14.2	14.0	14.5	0.29
40	17.0	16.8	17.2	0.27
50	19.5	19.3	19.7	0.23
75	24.3	24.0	24.6	0.15
100	27.3	26.8	27.7	0.09
125	29.0	28.4	29.5	0.05
150	29.9	29.3	30.5	0.03
175	30.4	29.8	31.0	0.01

rough estimate of 3.1 d obtained from the laboratory data (Lough et al. footnote 7).

The first larva with 3 increments observed during the laboratory-rearing occurred on day 16 after estimated hatch. The mean age of fish with 3 increments cannot be estimated directly because sampling stopped after 18 d. But assuming a range of ages of 12 d (4 standard deviations), the mean age of a 3-increment larva would be approximately 22 d. Assuming daily increment deposition for the population after the third increment, a 7-increment larva would have an average age of 26 d, which compares well with the field estimate of 25 d.

Messieh and Moore (footnote 9), working with autumn-spawned herring larvae in the Gulf of St. Lawrence, recently estimated the age of larvae at the time of the nuclear check completion to be 15-17 d from hatching on average.

Growth Curve Compared with Other Field Studies

Direct observations of herring egg beds by divers were made on Jeffreys Ledge, Gulf of Maine, in 1974 by Cooper et al. (footnote 3). Spawning occurred between 29 September and 3 October 1974 at about 35-50 m depth when the bottom water temperature was 9.6°C. Larval hatching began on this site on 6 October and was completed by 11 October, a 5-d period. Careful visual examination of the egg bed by the divers suggested that major hatching began on 7-8 October. Newly hatched larvae collected on the egg bed have already been reported in Table 3 to have a mean Formalin-preserved length of 5.7 mm (0.5 mm SD). A special 24-h vertical series of plankton hauls was made slightly downstream of the egg bed 11-12 October (*Delaware II* 74-12). The mean Formalin-preserved length of all larvae collected by day and night hauls was 6.7 mm (0.6 mm SD) (Lough and Cohen¹⁰). Approximately 4 d transpired between the middates of maximum hatching and their collection by the 24-h vertical study yielding an average growth rate of 0.25 mm/d. According to the fitted Gompertz growth curve (Table 4), 4-d-old larvae are estimated to have reached a mean length of 6.7 mm at a mean growth rate of 0.26 mm/d (range: 0.25-0.27 mm/d) which are essentially the same as the field estimates.

Graham and Chenoweth (1973) made direct observations of larval herring over egg beds on northeastern Georges Bank during autumn 1973. Submersible observations indicated that hatching occurred between 25 September and 5 October, a 10-d period. Larvae hatched in seawater from eggs brought on shipboard 27 September varied in length from 5 to 7 mm with over 90% at 6 mm. On 1 October, larvae collected within the vicinity of the egg beds varied from 5 to 9 mm in length but the mean was 7.1 mm about 4 d from hatching (27 September-1 October). Growth rate of these recently hatched larvae over the 4 d was estimated to be 0.28 mm/d, which is slightly higher but still comparable with the fitted growth curve.

Growth of larval herring based on the Gom-

pertz curve was 0.25 mm/d at hatch, increased to 0.30 mm/d at 20 d, and declined thereafter to <0.15 mm/d after 75 d. The average growth rate over 150 d from hatch was 0.20 mm/d which is similar to average seasonal estimates found in most other studies of herring larvae. By following length-frequency modes for Georges Bank-Nantucket Shoals herring larvae collected on the 1971-78 ICNAF surveys, Lough et al. (footnote 4) found an average rate of 0.195 mm/d as the best compromise to describe average growth over the 7-30 mm size classes (163 d). Boyar et al. (1973) estimated larval herring growth in the Georges Bank-Gulf of Maine region, September-June, to average 0.17 mm/d with a range of 0.14-0.25 mm/d. The form of the growth curve appears to be universal for herring larvae with a cessation in growth most noticeable during mid-larval life before increasing rapidly again at the time of metamorphosis. When Sette (1943) replotted the Clyde Sea, spring-spawned larval herring data of Marshall et al. (1937), he concluded that two logarithmic curves provided a better description of growth with a decrease in slope at a length of 19.5 mm. Graham et al. (1972) also showed a decrease in growth after about 20 mm for autumn-spawned herring larvae along the coastal western Gulf of Maine. Townsend and Graham (1981) followed two groups of larvae that entered the Sheepscot River estuary of Maine that grew about 0.2-0.3 mm/d from October to early January and from late February to early March, but experienced similar cessation of growth from late January to early February. Das (1968, 1972) followed length modes of Bay of Fundy-Gulf of Maine area herring larvae from hatching in September and estimated growth rates to be 0.29 mm/d in the autumn, gradually declining to <0.14 mm/d during late autumn and winter months, and then increasing geometrically to >0.36 mm/d in the spring and early summer. Messieh and Moore (footnote 9) also reported a rapid increase in growth at metamorphosis for herring larvae collected in the Gulf of St. Lawrence.

DISCUSSION

The available data indicate that the age and growth of herring larvae in the Gulf of Maine-Georges Bank region can be accurately estimated from otolith microstructure, although we have no direct evidence of the increment-day relation. A Gompertz growth curve fitted to the

¹⁰Lough, R. G., and R. E. Cohen. 1982. Vertical distribution of recently-hatched herring larvae and associated zooplankton on Jeffreys Ledge and Georges Bank, October 1974. Lab. Ref. 82-10. Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

field-caught larvae, which describes the length at age from an initial mean hatching size of 5.7 mm to an upper asymptotic mean length of 30.9 mm, agrees well with average growth rate estimates from other studies. Our field data begin with a 7-increment larva of 12.6 mm SL, which also is nearly identical to the mean length at increment age estimated by the growth curve. From the growth model a 7-increment larva is estimated to be on average 25 d from hatch (5.7 mm) having grown at an average rate of 0.28 mm/d. This implies that increment deposition does not occur daily over these 25 d or that variation in the timing of first increment deposition is high. If one assumes daily increment deposition from yolk-sac resorption (4.5 d), a 7-increment larva would be 11.5 d old, inferring the larva has grown at an average rate of 0.60 mm/d, which is rather high based on field and laboratory estimates. Herring larvae <15 mm have estimated growth rates typically in the range of 0.25-0.30 mm/d with an upper limit of about 0.35 mm/d.

The apparent delay in increment formation observed in the laboratory-reared herring larvae after the first increment at yolk-sac resorption may be due to rearing conditions, although we have no reason to suspect they were less than optimal. Other studies have shown that the formation of daily growth increments can be affected by variations in food ration, temperature, light-dark cycle, age of fish, and stressful conditions in general (see references in first section of paper). Increment formation appears to be species-specific and, for clupeoid species like *Engraulis mordax* (Brothers et al. 1976) and *Clupea harengus* (this study) with relatively small eggs and short incubation period, the initial increments begin at the time of yolk-sac resorption (Radtke and Waiwood 1980). A dark band or check observed around the nucleus of most of the larval otoliths collected in the field, but not apparent in the laboratory-reared larvae, may correspond to the time of yolk-sac resorption as Radtke and Waiwood (1980) found for larval cod otoliths. The nuclear check may be the result of several thin increments grouped together. Uchiyama and Struhsaker (1981), working with Pacific tunas, found that countable growth increments were formed only when the fishes were fed to satiation throughout the day. The nuclear check and the succeeding 10 or so thin increments observed for the field-caught herring larvae may be related to the inability of a first-feeding larva to meet its maximum daily ration

during the transition from its yolk supply to exogenous feeding. Initial feeding efficiency is low for herring larvae, <5% success at yolk-sac resorption, but increases to about 40% 2 wk after hatching and 70% after 5 wk (Blaxter and Staines 1971). Farris (1959) observed a rapid leveling off of growth after hatch in four species of fish and Zweifel and Lasker (1976), after fitting a two-stage Laird-Gompertz growth curve to a number of larval fish species, one from hatching to yolk-sac resorption and another to more rapid growth at the onset of feeding, suggested that this phenomenon was almost universal in larval growth. It is conceivable that during this period of reduced growth, increment deposition also may be delayed or diminished until the larva learns to capture sufficient numbers of prey and begins growing rapidly again.

Although larval herring appear to be very resistant to the range of temperatures normally encountered (Blaxter 1960), the effect of temperature on increment formation is not known. Water temperatures observed in herring spawning areas in the Gulf of Maine-Georges Bank region are typically as high as 12°-14°C in early autumn and decline to near 0°C in winter (Table 1), approaching their lower lethal limit (Graham and Davis 1971; Chenoweth 1970). Yolk-sac utilization in herring larvae is directly related to water temperature (Blaxter 1956; Blaxter and Hempel 1963, 1966; Blaxter and Ehrlich 1974) and variations in water temperature at hatch can reduce or extend the time to first feeding and consequently, otolith increment formation. Yolk-sac resorption is completed at 4-5 d at 10°C and 6 d at 8°C. Feeding of larvae is believed to commence at or prior to the end of yolk-sac resorption when the maximum body weight (excluding yolk sac) is reached after about 3 d at 8°C and 2 d at 12°C. Larvae reared at 10°C would initiate feeding 2-3 d after hatch. There is some evidence to indicate that early larval herring growth is better at higher temperatures (Blaxter 1962), although food availability is considered the more important factor in controlling growth processes and survival of larval fish in general (May 1974). Increment formation of the green sunfish, *Lepomis cyanellus*, could be stopped when growth was slowed sufficiently by simulated winter conditions (Taubert and Coble 1977). The slowing of growth during the winter period observed for larval herring in the Gulf of Maine-Georges Bank region also may affect their increment formation but further research will be required to

determine the effect of environmental variables on the relationship between otolith and larval growth.

ACKNOWLEDGMENTS

We thank P. Hamer and R. Cohen for their help with the laboratory and data processing. G. Laurence, NMFS Narragansett Laboratory, R.I., graciously provided the laboratory-reared larvae and unpublished experimental data used in this study. This report is MARMAP Contribution MED/NEFC 81-6.

LITERATURE CITED

- BARKMAN, R. C.
1978. The use of otolith growth rings to age young Atlantic silversides, *Menidia menidia*. Trans. Am. Fish. Soc. 107:790-792.
- BARKMAN, R. C., D. A. BENGSTON, AND A. D. BECK.
1981. Daily growth of the juvenile fish (*Menidia menidia*) in the natural habitat compared with that of juveniles reared in the laboratory. In R. Lasker and K. Sherman (editors), The early life history of fish: recent studies. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 178:324-326.
- BEYER, J. E., AND G. C. LAURENCE.
1981. Aspects of stochasticity in modelling growth and survival of clupeoid fish larvae. In R. Lasker and K. Sherman (editors), The early life history of fish: recent studies. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 178:17-23.
- BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.
- BLAXTER, J. H. S.
1956. Herring rearing—II. The effect of temperature and other factors on development. Mar. Res. Ser. Scott. Home Dep. 5, 19 p.
1960. The effect of extremes of temperature on herring larvae. J. Mar. Biol. Assoc. U.K. 39:605-608.
1962. Herring rearing—IV. Rearing beyond the yolk-sac stage. Mar. Res. Dep. Agric. Fish. Scotl. 1, 18 p.
- BLAXTER, J. H. S., AND K. F. EHRLICH.
1974. Changes in behavior during starvation of herring and plaice larvae. In J. H. S. Blaxter (editor), The early life of fish, p. 575-588. Springer-Verlag, Berl.
- BLAXTER, J. H. S., AND G. HEMPEL.
1963. The influence of egg size on herring larvae (*Clupea harengus* L.). J. Cons. Cons. Int. Explor. Mer 28:211-240.
1966. Utilization of yolk by herring larvae. J. Mar. Biol. Assoc. U.K. 46:219-234.
- BLAXTER, J. H. S., AND M. E. STAINES.
1971. Food searching potential in marine fish larvae. In D. J. Crisp (editor), Fourth European Marine Biology Symposium, p. 467-485. Cambridge Univ. Press, Cambridge.
- BOYAR, H. C., R. R. MARAK, F. E. PERKINS, AND R. A. CLIFFORD.
1973. Seasonal distribution and growth of larval herring (*Clupea harengus* L.) in the Georges Bank-Gulf of Maine area from 1962 to 1970. J. Cons. Cons. Int. Explor. Mer 35:36-51.
- BROTHERS, E. B.
1981. What can otolith microstructure tell us about daily and subdaily events in the early life history of fish? In R. Lasker and K. Sherman (editors), The early life history of fish: recent studies. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 178:393-394.
- BROTHERS, E. B., C. P. MATHEWS, AND R. LASKER.
1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull., U.S. 74:1-8.
- BROTHERS, E. B., AND W. N. MCFARLAND.
1981. Correlations between otolith microstructure, growth, and life history transitions in newly recruited French grunts [*Haemulon flavolineatum* (Desmarest), *Haemulidae*]. In R. Lasker and K. Sherman (editors), The early life history of fish: recent studies. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 178:369-374.
- BUMPUS, D. F.
1976. Review of the physical oceanography of Georges Bank. Int. Comm. Northwest Atl. Fish. Res. Bull. 12:119-134.
- CHENOWETH, S. B.
1970. Seasonal variations in condition of larval herring in Boothbay area of the Maine Coast. J. Fish. Res. Board Can. 27:1875-1879.
- DAS, N.
1968. Spawning, distribution, survival, and growth of larval herring (*Clupea harengus* L.) in relation to hydrographic conditions in the Bay of Fundy. Fish. Res. Board Can., Tech. Rep. 88, 129 p.
1972. Growth of larval herring (*Clupea harengus*) in the Bay of Fundy and Gulf of Maine area. J. Fish. Res. Board Can. 29:573-575.
- DOYLE, M. J.
1977. A morphological staging system for the larval development of the herring, *Clupea harengus* L. J. Mar. Biol. Assoc. U.K. 57:859-867.
- EHRlich, K. F., J. H. S. BLAXTER, AND R. PEMBERTON.
1976. Morphological and histological changes during the growth and starvation of herring and plaice larvae. Mar. Biol. (Berl.) 35:105-118.
- FARRIS, D. A.
1959. A change in the early growth rates of four larval marine fishes. Limnol. Oceanogr. 4:29-36.
- GRAHAM, J. J., AND S. B. CHENOWETH.
1973. Distribution and abundance of larval herring, *Clupea harengus harengus* Linnaeus, over egg beds on Georges Bank. Int. Comm. Northwest Atl. Fish. Res. Bull. 10:141-149.
- GRAHAM, J. J., S. B. CHENOWETH, AND C. W. DAVIS.
1972. Abundance, distribution, movements, and lengths of larval herring along the western coast of the Gulf of Maine. Fish. Bull., U.S. 70:307-321.
- GRAHAM, J. J., AND C. W. DAVIS.
1971. Estimates of mortality and year-class strength of larval herring in western Maine, 1964-67. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 160:147-152.
- HEMPEL, G.
1959. Zum Wachstum der Otolithen bei Jungheringen. Helgol. Wiss. Meeresunter. 6:241-259.
- KRAMER, D., AND J. R. ZWEIFEL.
1970. Growth of anchovy larvae (*Engraulis mordax* Girard) in the laboratory as influenced by temperature. Calif. Coop. Oceanic Fish. Invest. Rep. 14:84-87.

- LAIRD, A. K.
1969. The dynamics of growth. *Res./Dev.* 20(8):28-31.
- LOUGH, R. G., G. R. BOLZ, M. D. GROSSLEIN, AND D. C. POTTER.
1981. Abundance and survival of sea herring (*Clupea harengus* L.) larvae in relation to environmental factors, spawning stock size, and recruitment for the Georges Bank area, 1968-77. In R. Lasker and K. Sherman (editors), The early life history of fish: recent studies. *Rapp. P.-V. Réun. Cons. Int. Explor. Mer* 178:220-222.
- MARSHALL, S. M., A. G. NICHOLLS, AND A. P. ORR.
1937. On the growth and feeding of the larval and post-larval stages of the Clyde herring. *J. Mar. Biol. Assoc. U.K.* 22:245-268.
- MAY, R. C.
1974. Larval mortality in marine fishes and the critical period concept. In J. H. S. Blaxter (editor), The early life history of fish, p. 3-19. Springer-Verlag, Berl.
- MESSIEH, S. N.
1975. Growth of the otoliths of young herring in the Bay of Fundy. *Trans. Am. Fish. Soc.* 104:770-772.
- METHOT, R. D.
1981. Spatial covariation of daily growth rates of larval northern anchovy, *Engraulis mordax*, and northern lampfish, *Stenobrachius leucopsarus*. In R. Lasker and K. Sherman (editors), The early life history of fish: recent studies. *Rapp. P.-V. Réun. Cons. Int. Explor. Mer* 178:424-431.
- METHOT, R. D., JR., AND D. KRAMER.
1979. Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. *Fish. Bull., U.S.* 77:413-423.
- PANNELLA, G.
1971. Fish otoliths: daily growth layers and periodical patterns. *Science (Wash., D.C.)* 173:1124-1127.
1974. Otolith growth patterns: an aid in age determination in temperate and tropical fishes. In T. B. Bagenal (editor), Proceedings of an international symposium on the ageing of fish, p. 28-39. Unwin Brothers, Surrey, Engl.
- PENNINGTON, M. R.
1979. Fitting a growth curve to field data. In J. K. Ord, G. P. Patil, and C. Taillie (editors), Statistical distributions in ecological work, p. 419-428. Int. Coop. Publ. House, Fairland, Md.
- RADTKE, R. L., AND K. G. WAIWOOD.
1980. Otolith formation and body shrinkage due to fixation in larval cod (*Gadus morhua*). *Can. Tech. Rep. Fish. Aquat. Sci.* 929, 10 p.
- RALSTON, S.
1976. Age determination of a tropical reef butterflyfish utilizing daily growth rings of otoliths. *Fish. Bull., U.S.* 74:990-994.
- SAKAWAGA, G. T., AND M. KIMURA.
1976. Growth of laboratory-reared northern anchovy, *Engraulis mordax*, from southern California. *Fish. Bull., U.S.* 74:271-279.
- SAMEOTO, D. D.
1972. Distribution of herring (*Clupea harengus*) larvae along the southern coast of Nova Scotia with observations on their growth and condition factor. *J. Fish. Res. Board Can.* 29:507-515.
- SCOTT, J. S.
1973. Otolith structure and growth in northern sand lance, *Ammodytes dubius*, from the Scotian Shelf. *Int. Comm. Northwest Atl. Fish. Res. Bull.* 10:107-115.
- SETTE, O. E.
1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part I: Early life history, including growth, drift, and mortality of the egg and larval population. *U.S. Fish Wildl. Serv., Fish. Bull.* 50:149-237.
- SHERMAN, K.
1980. MARMAP, a fisheries ecosystem study in the Northwest Atlantic: Fluctuations in ichthyoplankton-zooplankton components and their potential for impact on the system. In F. P. Diemer, F. J. Vernberg, and D. Z. Mirkes (editors), Advanced concepts in ocean measurements for marine biology, p. 9-37. Belle W. Baruch Institute for Marine Biology and Coastal Research. Univ. S.C. Press, Columbia.
- STEFFENSEN, E.
1980. Daily growth increments observed in otoliths from juvenile East Baltic cod. *Dana* 1:29-37.
- STRUHSAKER, P., AND J. H. UCHIYAMA.
1976. Age and growth of the nehu, *Stolephorus purpurus* (Pisces: Engraulidae), from the Hawaiian Islands as indicated by daily growth increments of sagittae. *Fish. Bull., U.S.* 74:9-17.
- TAUBERT, B. D., AND D. W. COBLE.
1977. Daily rings in otoliths of three species of *Lepomis* and *Tilapia mossambica*. *J. Fish. Res. Board Can.* 34:332-340.
- THEILACKER, G. H.
1980. Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation. *Fish. Bull., U.S.* 78:685-692.
- TIBBO, S. N., AND J. E. HENRI LEGARÉ.
1960. Further study of larval herring (*Clupea harengus* L.) in the Bay of Fundy and Gulf of Maine. *J. Fish. Res. Board Can.* 17:933-942.
- TIBBO, S. N., J. E. HENRI LEGARÉ, L. W. SCATTERGOOD, AND R. F. TEMPLE.
1958. On the occurrence and distribution of larval herring (*Clupea harengus* L.) in the Bay of Fundy and the Gulf of Maine. *J. Fish. Res. Board Can.* 15:1451-1469.
- TOWNSEND, D. W., AND J. J. GRAHAM.
1981. Growth and age structure of larval Atlantic herring, *Clupea harengus harengus*, in the Sheepscoot River estuary, Maine, as determined by daily growth increments in otoliths. *Fish. Bull., U.S.* 79:123-130.
- UCHIYAMA, J. H., AND P. STRUHSAKER.
1981. Age and growth of skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, as indicated by daily growth increments of sagittae. *Fish. Bull., U.S.* 79:151-162.
- WATSON, J. E.
1964. Determining the age of young herring from their otoliths. *Trans. Am. Fish. Soc.* 93:11-20.
- WILSON, K. H., AND P. A. LARKIN.
1980. Daily growth rings in the otoliths of juvenile sockeye salmon (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.* 37:1495-1498.
- ZWEIFEL, J. R., AND R. LASKER.
1976. Prehatch and posthatch growth of fishes—a general model. *Fish. Bull., U.S.* 74:609-621.