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A Growth Model for Larval Herring (*Clupea harengus* L.) in the Georges Bank-Gulf of Maine Area Based on Otolith Growth Increments[1]

by

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ABSTRACT

The mean growth of herring larvae from hatch to metamorphosis is described by a Gompertz growth curve fitted to 311 autumn-spawned, field-collected specimens. The decaying exponential growth model describes the length at age (based on a range of 7-160 otolith increments) from an initial mean hatching size of 5.66 mm through an inflection point of 11.28 mm at 20.28 days to an upper asymtotic limit (30.895 mm) of mean growth at 175 days. A larvae with 7 otolith increments is estimated from the growth model to be 25 days old. Other field and laboratory evidence is consistent with this relationship. Larvae reared in the laboratory at 10°C from fertilized eggs began initial increment deposition 4.5 days post hatch near the end of yolk-sac absorption. However, formation of the 2nd increment was delayed 7.5 days from the initial increment and the 3rd increment was estimated to be delayed 10 days from the 2nd increment. The standard deviation of age for a fixed number of increments is approximately 3 days and appears to be independent of the number of increments. Laboratory and field studies support the assumption that increment deposition becomes daily after the 3rd increment.

INTRODUCTION

The development of a precise growth model for larval herring requires a means of accurately aging the larvae. Recently, techniques have become available for accurate aging of larval and adult fishes based on daily growth increments or lamellae in their otoliths, thus providing a detailed chronological record of events in the growth history of an individual fish (Panella 1972, 1974, Brothers et al. 1976, Struhsaker and Uchiyama 1976, Ralston 1976, Taubert and Coble 1977, Barkman 1978, Methot and Kramer 1979, Brothers and McFarland 1979, Barkman et al. 1979). In fact, daily, as well as annual growth layers appear to be a universal phenomenon found throughout the animal and plant kingdoms (Neville 1967).

The objective of this study is to describe the growth of larval herring collected in the Georges Bank - Gulf of Maine area from hatching to metamorphosis, essentially the first six months of life, by fitting a Gompertz growth curve to length at age data based on "daily" growth increments in their otoliths. Evidence for the presence of apparent daily otolith growth increments in larval herring and their applicability for estimating growth rates was given in a preliminary report by Rosenberg and Lough (1977). The statistical treatment for fitting a Gompertz growth curve to the field-collected larval herring data used in this paper is provided in detail by Pennington (1979). Previous use of the Gompertz model to describe growth of larval fishes was made by Kramer and Zweifel (1970), Sakagawa and Kimura (1976), Zwiefel and Lasker (1976), and Methot and Kramer (1979).

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[1] A complete version of this manuscript has been submitted to US FISHERY BULLETIN.

METHODS

Larval herring for otolith studies were collected at selected stations within a standard grid of sampling stations 15-20 miles apart from 5 ICNAF[1] larval herring surveys conducted from October 1976 through March 1977 along the western Gulf of Maine, Georges Bank, and Nantucket Shoals (Table 1). Larvae normally were collected at stations where high densities were encountered. Sampling of larvae was made using a 61-cm bongo net (mesh sizes of 0.505- and 0.333-mm) to a maximum depth of 100 m, while the vessel was underway at 3.5 knots. Further details of the sampling gear and protocols can be found in Lough and Bolz (1979). Immediately after the nets were brought aboard the vessel, larvae were sorted from the untreated 0.505-mm mesh plankton sample and frozen in petrie dishes.

In order to determine the precise age when increment deposition first begins in larval herring otoliths, larvae were reared from fertilized eggs in the laboratory. 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 NOAA, 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 (1979) and fed wild plankton at high densities ($>3/ml^{-1}$). Approximately 15 larvae were removed from the rearing aquaria daily from hatch 28 October through 15 November and immediately 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 0.01 mm. Otoliths (sagittae) were removed from both sides of the head when possible and mounted in Canada balsam or Permount. The otoliths were whole mounted and little difficulty was found in reading the bones intact so that further preparation was unnecessary.

Counts of field-collected and lab-reared otolith growth increments were made using a compound microscope-video system with a magnification range of 630X for the largest otoliths and 1000X or 2000X for the smallest. A minimum of 3 counts were made on all otoliths or repeated until a mean value was reached with a maximum acceptable range of 5% variability. Selected otoliths were photographed and inter-ring distances were measured across a posterior radius from the nucleus with an electronic digitizer.

All field-collected larvae used for otolith ageing were frozen, whereas all lab-reared larvae used for corroborative information were preserved in 75% ethyl alcohol. Theilacker (1980) reports 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 less than 11 mm SL net-treated for 20 minutes could shrink as much as 18% of their live length prior to preservation. An additional 3% shrinkage due to 5% Formalin preservation was recommended for all body parts after net-treatment, whereas preservation in 80% ethyl alcohol did not cause any additional shrinkage in standard length. Engel's (1977) study indicated that freezing changed the length of fish approximately the same as Formalin preservation. However, net-treatment of larvae usually accounts for the greater percentage of shrinkage. No correction factor was applied to our field-collected data because Theilacker's results for anchovy larvae may not apply and we do have a similar net-preservation treatment study for larval herring. We do not feel that the Gompertz population estimated growth curve fit applied to the uncorrected field-collected larvae would be significantly altered with respect to shape compared to corrected data. When a directed comparison is made in this paper between the lengths of lab-reared and field estimated larval lengths, a correction factor applied to the lab data will be specified. From our experience we estimate that nearly all larvae collected on ICNAF surveys have been dead for at least 20 min prior to preservation.

[1] International Commission for the Northwest Atlantic Fisheries--now NAFO: Northwest Atlantic Fisheries Organization.

RESULTS

Otoliths from 311 herring larvae caught in plankton hauls were processed in this study covering the first six months of life of the 1976 spawning season. The only significant gap in time in our collection of larval otolith data was from mid-December 1976 to mid-February 1977. ICNAF surveys have never been conducted during the month of January. Also, we were not able to collect any recently-hatched larvae less than 10 mm length for otoliths on these surveys and therefore resorted to lab-reared larvae for the smallest size.

Larval herring otoliths are essentially spherical with a slight protuberance at the anterior edge from which further elongation occurs developing into the adult rostrum (Figure 1). According to Hempel (1959) the typical outline of the adult herring otolith is reached at about 90 mm total length. The otolith nucleus at hatch has a mean lateral diameter of 22 μm and all nuclei examined were of the hyaline type which is characteristic of nearly all autumn spawners in the Gulf of Maine - Georges Bank area (Watson 1964). Growth increments are deposted around the nucleus as successive dark and light bands. Distinctive, darker than normal growth bands were noted, but they did not appear to be formed with any pattern or complex periodicity as observed by Pannella (1971), nor was there any evidence of subdaily rings as observed in some other species by Taubert and Coble (1976), Brothers and McFarland (1979).

Various allometric relationships were analyzed among standard length, head length, otolith size and number of increments by station and area. No significant differences could be observed in these relationships between stations or areas (Georges Bank vs Nantucket Shoals vs Gulf of Maine). Therefore the data are pooled.

In Table 2 the pooled data are summarized as the number of otolith increments per unit standard length. Larvae from the field collections ranged in length from 11.0 to 35.0 mm and otolith increments ranged from 7 to 160. Standard length and number of increments increased in a linear fashion up to about 20 mm. Thereafter, standard length did not increase as rapidly as the number of increments.

Lab-reared larvae

Herring eggs were fertilized 17 October 1978 and held in the laboratory at 10°C, and hatching occurred over a 5-day period. Fifty-percent hatch was estimated to occur on 28 October with a mean incubation time of 11 days. Yolk-sac absorption was estimated to be 50% complete 4-5 days after hatching, and 99% complete 6 days after hatching. Age in days from hatching midpoint for larvae with 0-3 otolith growth increments is shown in Figure 2. The 1st increment appeared on larval otoliths that ranged in age from 0 to 9 days from hatch with a middate of 4.5 days which indicates that the 1st increment is deposited near the end of yolk-sac absorption. Larvae were staged according to Doyle (1977) and there was a progression of three substages 1a-1c over the first 3 days from hatch so that after the 3rd day only remnants of yolk-sac remained.

The 2nd growth increment occurred in larvae 6-18+ days old for a middate of 12 days from hatch or, 7.5 days from the middate of the 1st increment formation. The 3rd increment was observed for the first time on a larva 16 days from hatch, but unfortunately the experiment was terminated before the complete age distribution of 3-increment larvae could be determined. If the age distribution of 3-increment larvae is the same as the 2-increment larvae of 12 days, then the estimated age of 3-increment larvae would range from 16-28 days with a middate of 22 days from hatch.

The delay of 7.5 days between the 1st and 2nd growth increments and an estimated 10-day delay between the 2nd and 3rd increments does not agree with previous studies indicating daily increment deposition after the 1st increment. Two possibilities are proposed: (1) increment deposition after the 1st increment was delayed because of the laboratory rearing conditions (e.g., lack of suitable food), or (2) increment deposition is normally delayed after the 1st increment but becomes a daily process at some later point in time. Both offer plausible explanations and in the following sections of this paper we will attempt to address these questions through the development of a growth model

for larval herring and confirm the accuracy of this model with other supporting evidence in favor of the second explanation.

Growth of larvae

A Gompertz growth curve was fitted to the field-collected data to describe the mean growth of larval herring based on 311 specimens with otolith growth increments ranging from 7-160. Using the field data as a starting point it was assumed that increments were deposited daily after the 7th increment so that the equation

$$L = L_7 \, e^{k[1-e^{-\alpha(r-7)}]}$$

was taken to represent 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

$$L = 12.70 \, e^{0.889 \, [1-e^{-0.0261(r-7)}]} \qquad \text{for } r \geq 7 \qquad (1)$$

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

Equation (1) may be rewritten as:

$$L = 30.895 \, [e^{-1.067e^{-0.0261r}}] \qquad r \geq 7 \qquad (2)$$

where $30.895 = \hat{L}_\infty$, the asymptotic limit of mean growth during the October-March period. Assuming:

(i) for at least $r \geq 7$, increments are deposited daily

and

(ii) the curve (2) approximates growth from hatch,

then denoting age by x,

$$x = r+c \qquad r \geq 7$$

where c is an unknown constant,

or

$$r = x-c \qquad x \geq c+7$$

thus,

$$L = 30.895 \, e^{-1.067e^{-0.0261(x-c)}} \qquad x \geq c+7 \qquad (3)$$

which if assumption (ii) is reasonable, (3) holds for $x \geq 0$ where x=0 is the date of hatching.

Letting L_o denote mean length at hatch then,

$$L_o = 30.895 \, e^{-1.067e^{0.0261c}}$$

or,

$$c = \frac{\ln (3.431 - \ln L_o) - 0.0649}{0.0261}$$

Table 3 gives an estimate ($\hat{c}$) and the age of larvae with 7 increments ($\hat{c}+7$) derived from the mean length of recently hatched larvae collected on the Jeffreys Ledge spawning beds (Cooper et al. 1975).

For example, if L_o = 5.66 mm, then from equation (3) length as a function of age is

$$L = 30.895\ e^{-1.698e^{-0.026x}} \qquad x>0 \qquad (4)$$

From equation (4) the mean length, 95% confidence limits, and growth rate (mm/day) are estimated from hatch through 175 days and are given in Table 4. Also, the fitted growth curve is shown in Figure 3 with individual data points designated as to their origin. The following comments refer to Figure 4:

(1) The growth curve is based on data with more than 6 increments and a mean length of 5.66 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.

(2) By "sliding" the length axis to the right or left, the age of larvae with 7 increments can be estimated for different values of L_o.

(3) The curve has a point of inflection at x = 20.28 days. This is the point of maximum growth, i.e. ΔL is maximum at x = 20.28 days. In Table 4 one can inspect the growth rate column and see that growth increases from 0.251 mm/day at hatch (x=0) to 0.297 mm/day at 20 days, decreasing rapidly thereafter to 0.014 mm/day at 175 days.

(4) 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 of larvae alive at a given age.

(5) The spread of larvae originating from the three subareas appears to be uniformly distributed around the growth curve with the exception that Gulf of Maine larvae over a 100 days of age are mostly distributed below the growth curve, i.e., the Gulf of Maine larvae appears to reach a smaller size during the winter compared to larvae collected on Nantucket Shoals (Figure 4). However, a more plausible explanation is related to the fact that these larvae were collected in day hauls whereas the Nantucket Shoals larvae were collected evenly by both day and night hauls. It is a well known fact that larger larvae avoid plankton net hauls more effectively by day then by night. A close inspection of the distribution of day and night hauls around the growth curve (not shown here) reveals that smaller larvae are collected in day hauls for both young and old larvae, whereas larvae collected in night hauls are evenly distributed around the curve.

(6) The mean lengths at age of lab-reared larvae having 1 and 2 increments fall reasonably close to the curve near the origin. The mean length of the lab-reared larvae at hatch was reported by Beyer and Laurence (1979) to be 7.66 mm (S.D.=0.58 mm). After correcting for a 20-min net treatment and formalin preservation shrinkage factor to compare with the field-collected data, their reported mean hatching size is estimated to be 6.40 mm, which compares closely with the Jeffreys Ledge diver-collected, formalin preserved yolk-sac larvae of 5.66 mm mean SL.

Initial deposition of otolith increments

A larva with 7 increments is estimated from field data to be approximately 25 days old. The reasonableness of this relationship and other aspects of the growth of field larvae is briefly compared to the lab-reared larvae.

The mean age of lab-reared larvae from hatch with a fixed number of increments has already been reported on p. 4. Letting,

x_i be the age of ith larvae with r increments,

x_i' be the estimated age,

and

x_r be the mean age of larvae with r increments,

then

$$x_i' = x_i + \delta \quad (5)$$

and

$$x_i = x_r + \varepsilon \quad (6)$$

where δ and ε are random variables. The reason equation (5) is necessary is that age is not known precisely but was estimated from the point of 50% hatch; complete hatching of the laboratory population took 5 days.

From equations (5) and (6), (and assuming δ and ε are independent) the observed variability, var (x'), of age for a fixed number of increments is equal to

$$\text{var}(\delta) + \text{var}(\varepsilon).$$

Using the range of hatching (5 days), and assuming the range is roughly 4 standard deviations, an estimate of var (δ) is approximately equal to 1.5 days. Using the same rationale on the data from the lab-reared larvae, the var (x') is approximately 11 days. Hence,

$$\text{var}(\varepsilon) = \text{var}(x')-\text{var}(\delta)$$
$$= 11-1.5 = 9.5 \text{ days}.$$

that is $\sqrt{\text{var}(\varepsilon)}$, the standard deviation of age for a fixed number of increments is approximately 3.1 days, or for a fixed number of increments the ages range over roughly 12 days (see Figure 2, which shows x' versus the number of increments).

An estimate of $\sqrt{\text{var}(\varepsilon)}$ was made independently from the field data by Pennington (1979) and its value of 2.93 days compares closely to that obtained from the laboratory data. From these results it appears that $\sqrt{\text{var}(\varepsilon)}$ is fairly independent of the number of increments.

The first larva with 3 increments observed during the lab-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 days. But assuming a range of ages of 12 days, the mean age for 3 increment larvae would be approximately 22 days. Assuming daily increment deposition after the 3rd increment, a 7-increment larva would have an average age of 26 days, which again, considering the roughness of the approximations, compares fairly well with the field estimates.

In many of the otoliths examined from field-collected larvae the first 5-10 increments around the nucleus were observed to be thin and poorly defined, which would indicate a slow growth period. This weakly defined core of growth deposition from the field specimens may indeed reflect the initial slow (<1/day) increment formation for those larvae reared in the laboratory for 18 days. The thickness of the first 2 growth increments from the lab-reared larvae were consistently 0.8-1.0 μm, which compares closely with the initial increment thickness observed in field-collected larvae.

Growth curve compared to other field data

The Gompertz growth curve (equation 4) was compared to the 1976 season's larval herring survey length-frequency data for the Georges Bank - Nantucket Shoals area in Figure 4. The initial hatching time, corresponding to a length of 5.66 mm length, was estimated by extrapolating backwards through time from the growth model from the first surveys (24 October 1976 middate) mean larval length of 12.7 mm. A hatching date of 1 October was estimated by this method which is reasonable based on previous years spawning dates. The projected

growth curve intersects the 95% confidence bands for the mean size of larvae on each of the other three surveys in November, December, and February. The mean and modal length frequencies for all surveys essentially correspond with one another, not being more than 1 mm apart. Detailed length-frequency distributions for these surveys can be found in Lough and Bolz (1979). The February mean length lies somewhat more above the growth curve, although not significantly so in terms of length, and this difference may reflect sampling of different larval populations by the two studies. It has already been indicated that a downward shift in the growth curve could result if larvae were collected more by day than night hauls. It is interesting to note that if the same growth curve was extrapolated back from the February mean length of 32.0 mm, then this would imply that only the larger larvae from each survey, or those spawned somewhat earlier in the season, survived through the winter.

Direct observations of herring egg beds by divers were made on Jeffreys Ledge, Gulf of Maine, in 1974 by Cooper et al. (1975). 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 6 October and was completed by 11 October, a 5-day period. Careful visual examination of the egg bed 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 preserved length of 5.66 mm (0.54 mm SD). A special 24-hour vertical series of plankton hauls was made slightly downstream of the egg bed 11-12 October (Delaware II 74-12). The mean length of all larvae collected was 6.65 mm (0.60 mm SD) (Lough and Cohen 1980). Approximately 4 days transpired between the middates of maximum hatching and their collection by the 24-hour vertical study. According to the fitted Gompertz growth curve, 4-day-old larvae are estimated to have a mean length of 6.69 mm which is remarkably close to the field estimate.

DISCUSSION

The Gompertz growth curve fitted to field-collected herring larvae agrees well with supporting field and laboratory data. The model describes the length at age, based on otolith increments, from an initial mean hatching size of 5.66 mm to an upper asymtotic mean growth of 30.895 mm near metamorphosis, with an inflection point at 20.28 days of age which corresponds to a length of 11.28 mm. When Sette (1943) replotted the Clyde Sea larval herring data of Marshall et al. (1937), he concluded that two logarithmic curves with a change in slope at a length of 19.5 mm, 30 days of age, provided a better description of larval herring growth. Subsequent studies have borne out the nonlinear nature of larval herring growth. Graham et al. (1972) also showed a decrease in growth after about 20 mm for autumn spawned herring collected along the coastal western Gulf of Maine. The change in larval herring growth pattern with time probably is related more to allometric growth of body depth, as opposed to length, rather than a leveling off of growth processes or change in feeding behavior. Body height/standard length ratios were estimated in this study to increase from ca. 0.04 for 10-25 mm (SL) herring larvae to ca 0.05 for 25-40 mm larvae. Length-weight relationships for larval herring through metamorphosis are essentially logarithmic (Laurence 1976, Ehrlich et al. 1976).

Growth of larval herring from the Gompertz model was estimated over 150 days to average 0.195 mm/day, increasing from 0.251 mm/day at hatch to ca. 0.297 mm at 20 days, and decreasing thereafter to <0.152 after 75 days. Das (1968) followed length modes of Bay of Fundy herring larvae from hatching in September and estimated growth rates to be 0.29 mm/day in early September, 0.21 mm/day in October and November, 0.14 mm/day over the winter, 0.21 mm/day in April, and 0.29 mm/day in May. Boyar et al. (1973) estimated larval herring growth in the Georges Bank - Gulf of Maine area from September through June to average 0.17 mm/day with a range of 0.14-0.25 mm/day. Lough et al. (1979), by following length-frequency modes for Georges Bank - Nantucket Shoals herring larvae collected on the ICNAF surveys, found an average rate of 0.20 mm/day as the best estimate to describe average growth from the 7 to 30 mm size classes (163 days). This average rate agrees reasonably well with field data on the time to grow from recently hatched larvae in October to a modal size of about 30 mm in February. Growth values for larvae collected on these autumn surveys ranged from 0.2 to 0.35 mm/day while values for larvae collected over the winter ranged from 0.1-0.2 mm/day. The average growth rate of Scottish herring larvae reared for 91 days through metamorphosis (35 mm TL) was reported by Ehrlich

et al. (1976) to be 0.22 mm/day. The Gompertz growth curve fitting in this paper does not apply to the spring period when larval herring growth probably increases again at the time of metamorphosis.

The Gompertz growth curve is exponential from hatch to the inflection point of 11.38 mm at 20.28 days with a decreasing growth rate thereafter; the curve represents a smooth transition without any marked point of decline in growth. Our field-collected otolith data essentially begins at the inflection point with a 7-increment larva of about 12.0 mm. The mean size of larvae at 4 days after hatching (the end of yolk-sac absorption and initial increment deposition) estimated from the model was corroborated with direct field observations to be 6.65 mm. However, we do not have direct evidence on the growth period corresponding with deposition of the 1st to the 7th increments. The lab-reared larvae showed a delay in increment formation after the initial deposition and between the 2nd and 3rd increments. By assuming daily increment formation after the 3rd increment, a 7-increment larva was estimated independently from the lab data to be 26 days old, which agrees closely with the Gompertz curve fitted field estimate of 25 days. If, instead, one assumes increment deposition is daily in the field after initiation then a 7-increment larva would be 11 days old. A 11-day old larva, to grow from 6.65 mm to 12.0 mm, would have an average growth rate of 0.49 mm/day, which is rather high based on previous field and laboratory estimates of growth for herring larvae. Larvae less than 15 mm have estimated growth rates typically in the range of 0.25-0.30 mm/day with an upper limit as high as 0.35 mm/day. At a rate of 0.25 mm/day, the estimated time to grow from 6.65 to 12.0 mm is 21 days, and at a rate of 0.35 mm/day, 15 days. Herring larvae reared by Laurence (1978 experiment, unpublished data), sampled daily from hatch to 6 days, grew from 7.17 mm (0.50 SD) to 8.74 mm (0.69 SD) (5.91 mm and 7.48 mm, resp., corrected for 20 min net treatment and formalin preservation) for a growth rate of 0.26 mm/day and compares well with the growth model estimate of 0.251 to 0.274 mm/day ($\bar{x}$ = 0.263 mm/day) over the same period (see Table 4).

It is not known with certainty if the initial delayed otolith growth increment formation observed in the lab-reared larvae is a regularly occurring phenomenon in wild larvae, although we have presented inferred evidence that this is the case. Unless more than 1 increment is deposited daily later in a larva's growth history, for which we have no evidence, increment deposition must be daily at some point after hatch because from field studies we know a larva of 20 mm SL is approximately 40-60 days of age. Based on the projected lab-reared increment deposition every 10 days, a larva of 50 days of age (20 mm) would have only about 6 increments. We have never observed 20 mm larvae from the field collections to have so few increments. Differences between otolith characteristics of wild and reared 0-group herring have been shown by Balbontin et al. (1973). Taubert and Coble (1977) and Methot and Kramer (1979) report that increment formation may be stopped when growth is slowed sufficiently by low temperature and lack of food, respectively, and then re-started when growth resumes. Methot and Kramer concluded after comparing lab-reared and field larval anchovy that wild larvae were growing fast enough to deposit a growth increment each day. For the lab-reared larval herring reported in this study, the 1st growth increment was formed near the end of yolk-sac absorption, 4.5 days from hatch. Deposition of the 1st increment is probably firmly fixed as the larva is existing primarily on its yolk reserves. A delay of 7.5 days was estimated between the 1st and 2nd growth increments and, perhaps 10 days between the 2nd and 3rd increments as well, which may be related to the ability of a first-feeding larva to meet its minimum daily ration during the transition from its yolk supply to planktonic organisms. In the rearing experiments reported by Beyer and Laurence (1979) which supplied the herring larvae used in this paper for otolith analysis, they report negative growth over the first 10 days of life, perhaps indicating some size-selective mortality. Even though these larvae were reared at optimum naupliar prey densities of 500/1, well above concentrations observed in the sea, the first-feeding larvae may still have required some additional microplankton component smaller than the copepod nauplii provided, and only survived because they were reared in the laboratory where there is essentially no predation mortality. Mortality in Laurence's (1978 experiment, unpublished data) batch of lab-reared larvae averaged 12%/day over 13 days with a noticeable increase in mortality after day 9, 6 days from the middate of yolk-sac absorption. First-feeding herring larvae reach the "point-of-no-return" about 6 days after yolk-sac absorption (Blaxter and Ehrlich 1974). However, high post yolk-sac mortality has been observed in the labor-

atory by other investigators (see Blaxter 1962) and perhaps is not an artifact of laboratory condition but reflects natural mortality that may be size-selective against the smaller, slower growing individuals. Farris (1959) observed a rapid leveling off of growth after hatch in four species of fish and Zweifel and Lasker (1976), after fitting a 2-stage Laird-Gompertz growth curve to a number of larval fish species, one from hatching to yolk-sac absorption, and another to more rapid growth at the onset of feeding, suggested that this phenomenon was almost universal in larval growth. Their larval growth curves pictured in Figure 3, p. 614, in fact, show negative growth of starved larvae several days after hatching. It is conceivable that during this period of reduced growth, increment deposition also may be delayed until the larva learns to capture sufficient numbers of prey and builds up its body reserves to begin growing rapidly again. Otolith increment formation in wild populations therefore, may normally be delayed or, for at least that portion of the slower-growing larvae.

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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 Georges Bank-Gulf of Maine area.

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
Annandale	76-01	38	43°37'	69°22'	W. Gulf of Maine	8 Oct. 1976	0300(N)	114	12.9	35
		44	43°44'	68°50'	" " " "	8 Oct.	1415(D)	76	13.0	39
		59	44°25'	67°35'	" " " "	9 Oct.	1515(D)	57	13.0	9
		65	44°36'	67°07'	" " " "	13 Oct.	0330(N)	85	12.7	37
Wieczno	76-03	72	41°45'	67°30'	Georges Bank	28 Oct.	0650(N)	42	13.8[1]	18
Researcher	76-01	42	41°54'	69°50'	Nantucket Shoals	1 Dec.	0002(N)	69	8.0	9
		35	41°21'	68°42'	Georges Bank	1 Dec.	0626(N)	108	8.6	3
		102	42°58'	70°00'	W. Gulf of Maine	8 Dec.	1030(N)	100	7.4	29
		105	43°30'	69°30'	" " " "	9 Dec.	1100(N)	150	7.5	12
		110	41°51'	66°15'	Georges Bank	11 Dec.	0955(N)	80	8.4	37
Mt. Mitchell	77-01	19	40°33'	70°20'	Nantucket Shoals	15 Feb. 1977	0701(N)	66	0.6	26
		20	40°45'	70°30'	" "	15 Feb.	1026(N)	65	0.0	2
		122	43°14'	70°01'	W. Gulf of Maine	24 Feb.	1620(D)	124	3.5	10
		123	43°00'	70°15'	" " " "	24 Feb.	1933(D)	166	3.0	10
Anton Dohrn	77-01	33	40°45'	69°30'	Nantucket Shoals	17 Mar.	2230(D)	47	4.3[1]	34

[1]Only surface temperature available.

Table 2. Number of otolith growth increments per unit standard length for larval herring collected in the Georges Bank - Gulf of Maine area, 1976 spawning season.

Length (mm)	No. otoliths	Mean no. increments	s.d.	Range
11.0	4	12.8	2.87	11-17
12.0	8	11.5	1.85	9-14
13.0	15	13.1	3.16	7-18
14.0	19	14.8	4.62	9-26
15.0	31	15.1	4.03	11-20
16.0	32	18.6	3.88	11-28
17.0	20	19.8	5.20	11-34
18.0	27	23.8	6.46	14-39
19.0	20	26.7	7.18	16-47
20.0	14	34.6	8.05	18-42
21.0	17	40.4	8.08	26-53
22.0	11	45.2	6.52	30-55
23.0	7	39.7	4.96	33-45
24.0	6	63.3	30.39	45-125
25.0	7	93.4	40.89	45-141
26.0	9	111.4	18.01	85-132
27.0	8	112.4	15.62	90-142
28.0	11	110.6	16.57	89-146
29.0	11	118.1	21.66	96-148
30.0	6	114.5	23.06	84-144
31.0	15	124.7	19.71	76-133
32.0	7	124.4	14.99	98-140
33.0	4	116.5	17.37	95-136
34.0	5	135.8	12.52	118-150
35.0	1	160.0	-----	-----

Table 3. Age ($\hat{c}$) of larval herring with 7 otolith growth increments ($\hat{c}$+7) estimated from an initial mean hatching size of 5.66 mm (0.54 mm one standard deviation) and 95% confidence intervals of the mean. Standard lengths of 100 newly hatched yolk-sac larvae (formalin preserved) were measured from egg bed samples collected by divers[1] on the Jeffreys Ledge study site (38 m depth), 8 October 1974.

Hatch length (L_o) mm	95% confidence intervals lower upper	$\hat{c}$ (days)	95% confidence intervals lower upper	Age of larva with 7 increments ($\hat{c}$ + 7 days)	95% confidence intervals lower upper
5.66	(5.55-5.77)	17.79	(17.36-18.22)	24.79	(24.36-25.22)

[1]Northeast 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/day) of larval herring from hatch through 175 days estimated from the Gompertz growth model fit.

Age (days)	Mean length (mm)	95% confidence limits lower	95% confidence limits upper	Growth rate (mm/day)
0	5.66	5.38	5.95	0.251
1	5.91	5.63	6.20	0.255
2	6.17	5.89	6.46	0.259
3	6.43	6.15	6.73	0.263
4	6.69	6.41	6.99	0.267
5	6.96	6.67	7.26	0.271
6	7.23	6.94	7.53	0.274
7	7.51	7.22	7.81	0.277
8	7.79	7.50	8.09	0.280
9	8.07	7.78	8.37	0.283
10	8.35	8.06	8.65	0.285
20	11.28	11.01	11.56	0.297
30	14.22	13.99	14.46	0.288
40	16.99	16.78	17.20	0.265
50	19.49	19.28	19.70	0.234
75	24.31	23.98	24.64	0.152
100	27.27	26.82	27.73	0.089
125	28.95	28.42	29.49	0.049
150	29.87	29.29	30.46	0.026
175	30.36	29.75	30.98	0.014

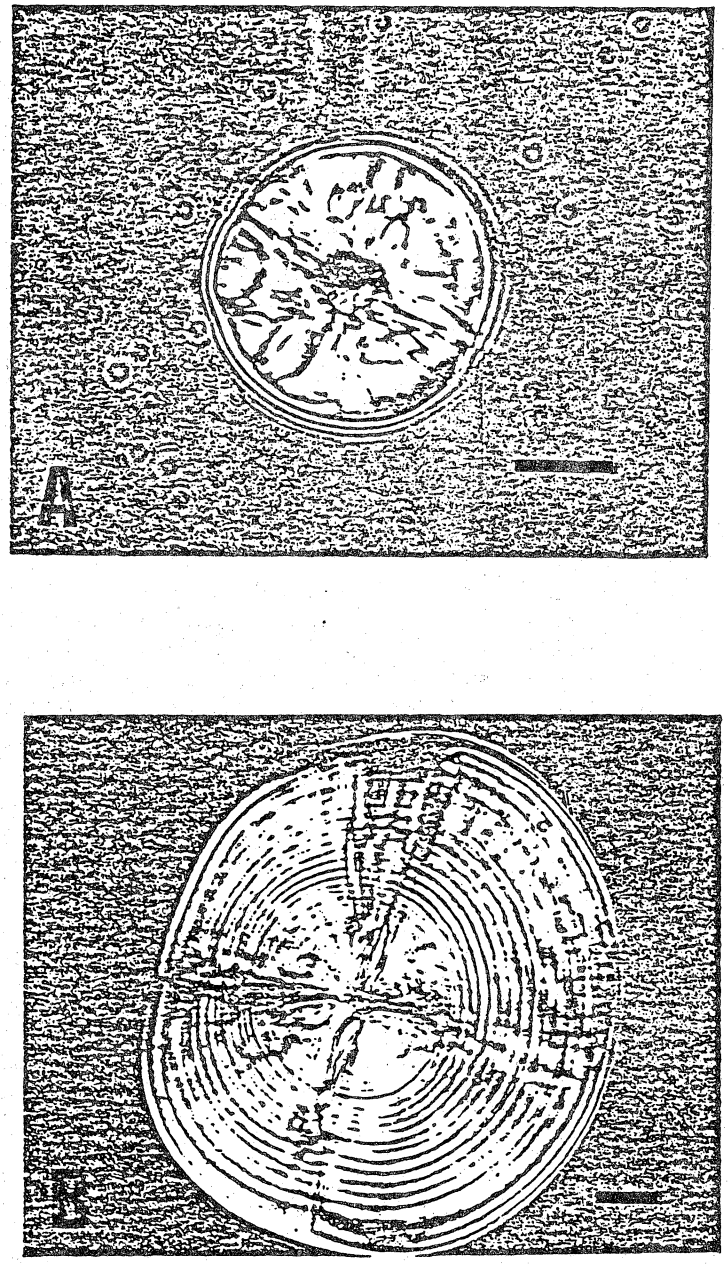

Figure 1. Sagittae of herring larvae; Clupea harengus. Bar on photographs represents 10 µm. A: otolith from lab-reared larva, 8.4 mm SL, showing 2 growth increments. B: otolith with 23 increments showing core of thin, poorly defined 7-10 increments around nucleus, 18.6 mm SL, Annandale 76-01, Sta. 38.

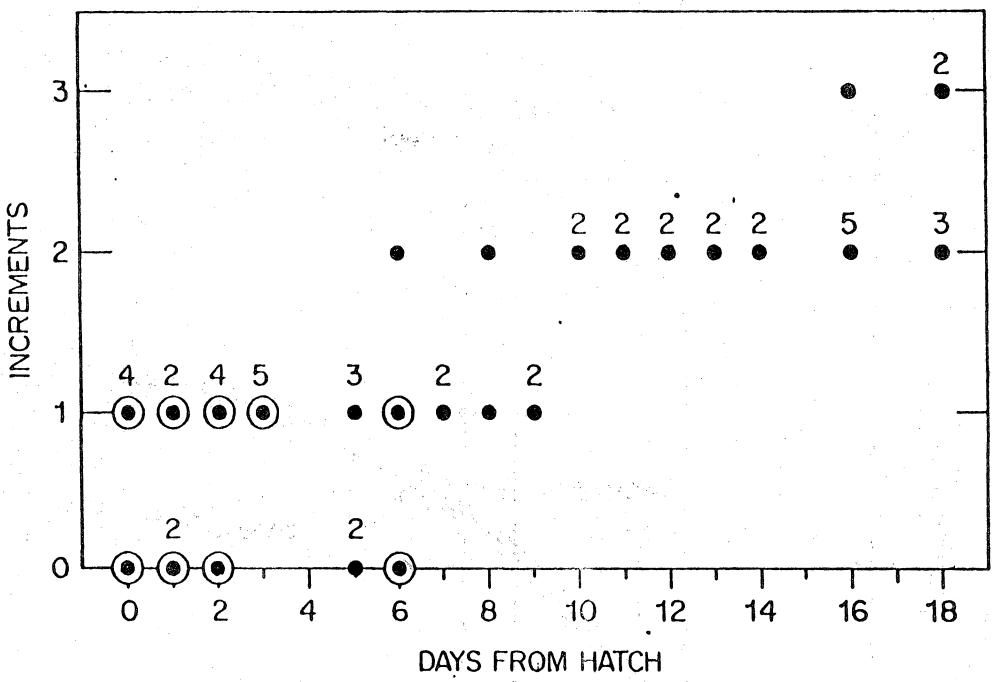

Figure 2. Otolith increment deposition for herring larvae sampled from 50% hatch through 18 days of rearing in the laboratory at 10°C. Encircled points represent yolk-sac larvae. Numbers above points denote numbers of larvae greater than one.

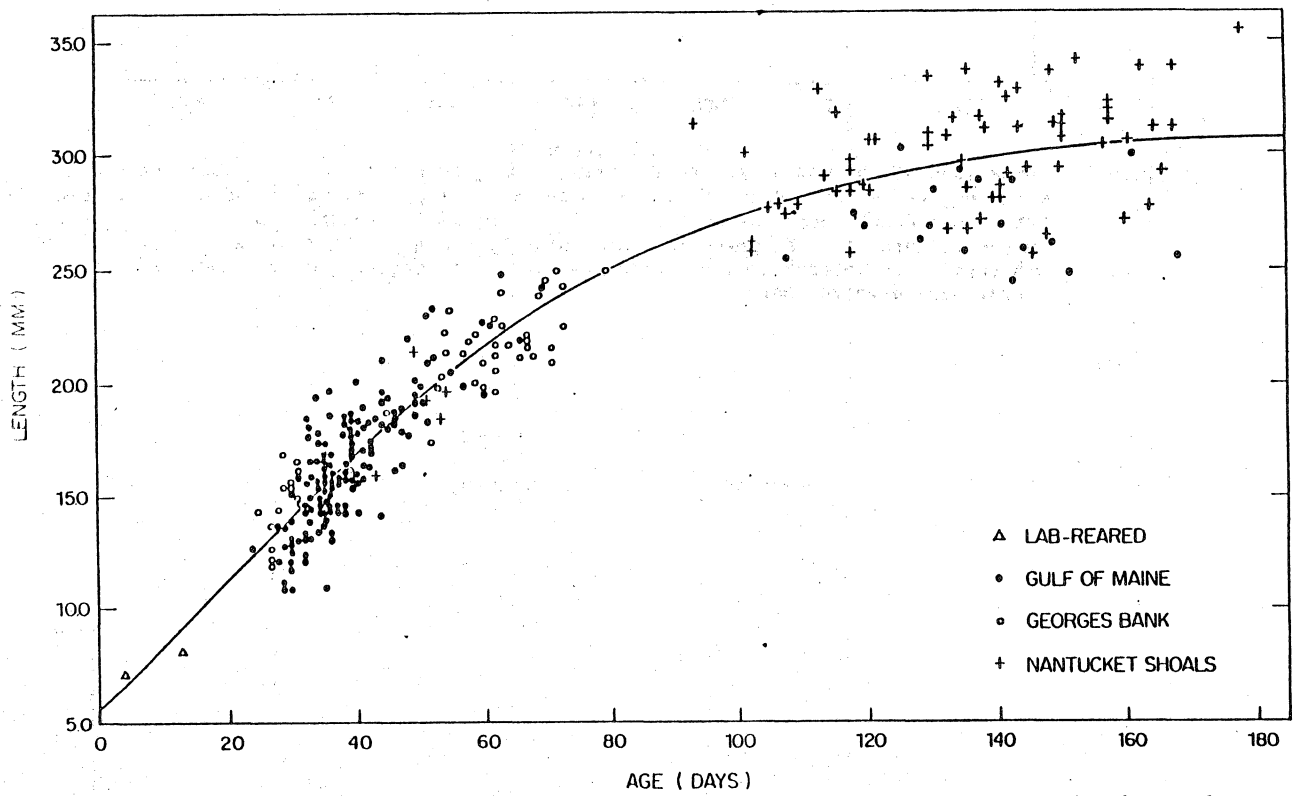

Figure 3. Gompertz growth curve fit to larval herring length at age data where mean hatch length L_o = 5.66 mm and asymtotic limit of mean growth, L_∞ = 30.895 mm. Individual data points are identified to their origin.

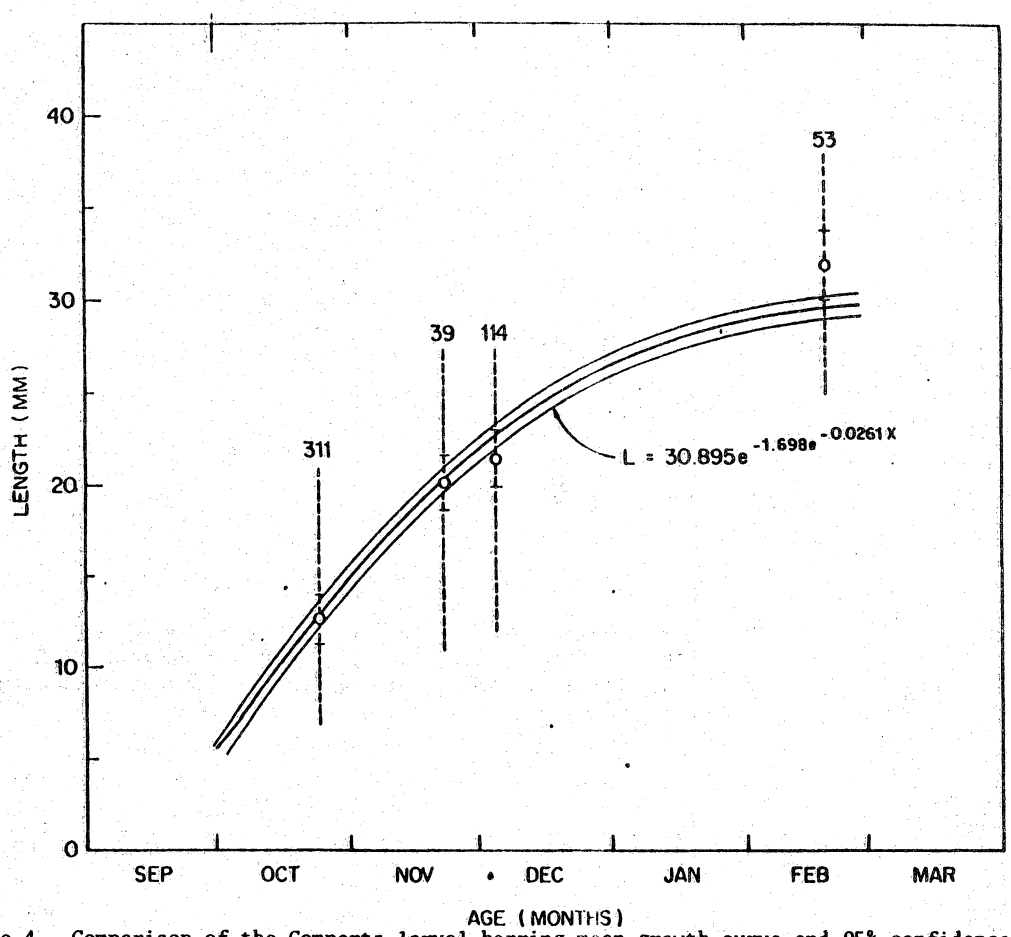

Figure 4. Comparison of the Gompertz larval herring mean growth curve and 95% confidence band with length-frequency data of larvae collected on four surveys conducted in the Georges Bank - Nantucket Shoals area, autumn 1976-winter 1977. Length-frequency data plotted on the middate of each survey is represented by the mean standard length(circle), and 95% confidence intervals within brackets, range of lengths (dotted line), and the sample size denoted above.