

**Abstract.**—Age and growth of 1,746 Atlantic herring, *Clupea harengus*, larvae collected in the Nantucket Shoals–Georges Bank region during the autumn–winter seasons of 1976–77, 1988–89, 1989–90, 1990–91, 1991–92, 1992–93, and 1993–94 were determined by enumerating the daily growth increments of their sagittal otoliths. Growth with respect to length for each of the years was best described by a Gompertz curve. Owing to severe weather events in November, January, and February of the 1976–77 season which disrupted the fishes' feeding regimen, growth was much slower (0.16 mm/d) than in more recent years. Lower daily food consumption was reflected in the rapid and continual decrease in otolith diameter during the autumn and winter of 1976. Growth for the other six years was strong, showed only minor interseasonal fluctuations (0.22–0.24 mm/d), and ranged intra-seasonally from a high of just over 0.40 mm/d in October to a low of 0.04 mm/d in February.

A general model of larval herring growth was constructed with data from six recent field seasons. Inverse regressive methods were employed to generate a composite growth curve with confidence limits for predicting age (days) for a given standard length (mm) from hatching until the onset of metamorphosis.

Analysis of otolith growth revealed a dramatic increase in the growth rate of the lapillus at about 2.5 months (29.0 mm). It is suggested that this increase may coincide with, or immediately follow, the filling of the otic bullae with gas and may provide an easily obtainable marker for estimating the timing of this critical event. The importance of this phase in the life of larval herring is discussed, particularly with reference to the 1976–77 season.

## Age and growth of larval Atlantic herring, *Clupea harengus*: a comparative study

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Based on the general assumption that fluctuations in the year-class strength of fish stocks are often determined by the rate of mortality during the first year of life (Hjort, 1914; May, 1974; Sissenwine, 1984), ichthyoplankton surveys have been conducted in the Nantucket Shoals–Georges Bank region for more than twenty years. From 1971 to 1979, research cruises designed to gain a better understanding of the early life history of Atlantic herring, *Clupea harengus*, and its relationship to recruitment and spawning stock size were undertaken monthly throughout the autumn and winter. These surveys were coordinated by the International Commission for the Northwest Atlantic Fisheries (ICNAF). The United States participation in the program was conducted concurrently as part of the MARMAP (Marine Resource Monitoring, Assessment, and Prediction) program of the Northeast Fisheries Science Center (Sherman, 1980). The MARMAP program was designed to measure long-term changes in the variability of larval fish abundance off the Northeast coast of the United States and is ongoing.

In the 1970's, intense fishing pressure by distant-water fleets led to a steady decrease in herring abundance on Georges Bank (An-

thony and Waring, 1980). Estimates of initial larval abundance declined by 95% from 1975 to 1976 (Lough et al., 1985). Herring populations in the region began to increase once again in the late 1980's, and this trend has continued into the 1990's (Smith and Morse, 1993). An examination of the age and growth of herring larvae, based on the enumeration of daily otolith increments, was initiated in 1976 (Lough et al., 1982). To understand better the recovery of Atlantic herring in the Georges Bank area, microstructural analysis of larval otoliths was incorporated as a routine procedure for each season beginning in the autumn of 1988. To date, otoliths from more than 1,700 larvae have been aged.

The primary goal of this study was to construct an age-at-length curve and a key for field-caught Atlantic herring larvae that describe their growth from hatch until onset of metamorphosis. Additionally, we compared larval growth during the autumn and winter of 1976–77 with that during six recent seasons of 1988–89, 1989–90, 1990–91, 1991–92, 1992–93, and 1993–94. Otolith growth was analyzed to determine whether changes in the fishes' daily food rations, attributable to severe weather, could be de-

tected (Methot, 1983; Karakiri et al., 1989; Maillet and Checkley, 1991). Estimated standard lengths at hatching and metamorphosis were calculated and compared.

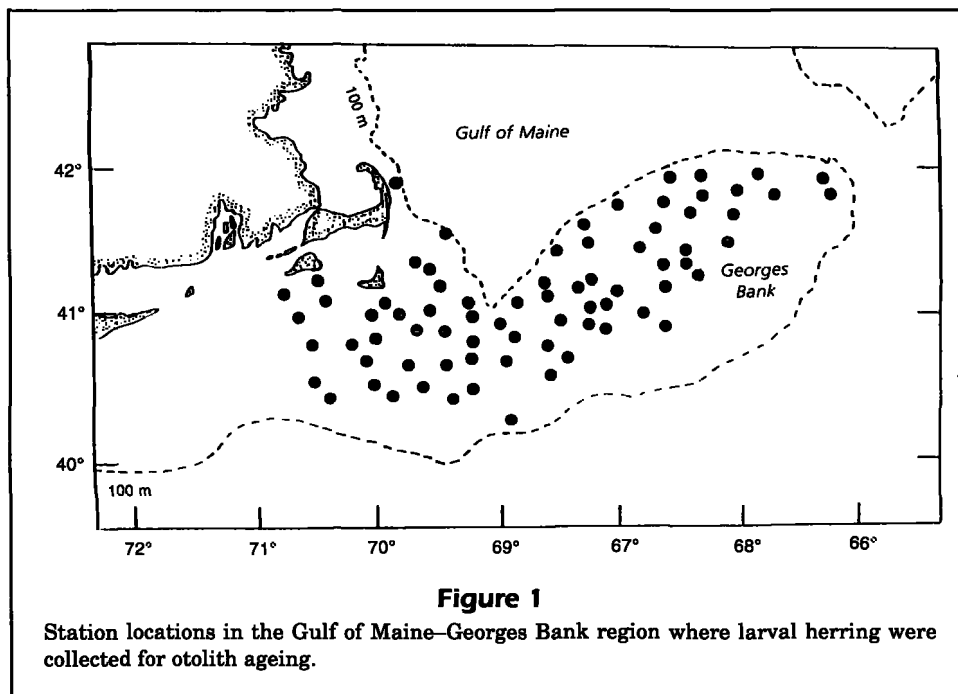
We also examined how developmental changes in the acoustico-lateralis system might relate to sensory thresholds that are critical in predator avoidance. Larval herring begin to demonstrate their characteristic C-shape startle response to environmental stimuli at a length of approximately 27–30 mm SL (Batty, 1989). This behavior does not become fully functional until the otic bullae are filled with air (22–30 mm), the air bladder and its connection to the acoustico-lateralis system are complete, and the larvae acquire the ability to swallow air at the surface (30–40 mm). Blaxter and Fuiman (1990) state that “filling the bullae with gas is probably the most significant event in the development of the anatomy of the sensory systems so far as predator evasion is concerned.” They observed that successful attacks by predators were reduced from 77% to 32% following the filling of the bullae. Without a mechanism to adjust the volume of air with pressure changes, the fish are restricted in their ability to migrate vertically, limiting their ability to search for prey, to avoid predators, and to control transport (Hoss et al., 1989). Because it is virtually impossible to determine the condition of the otic bullae in field-collected larvae, the otolith to fish-length relationship was analyzed to determine its usefulness in estimating the timing of this critical developmental landmark.

## Methods

Atlantic herring larvae were collected on 24 cruises at selected stations within a standard grid of sampling stations covering the western Gulf of Maine, Georges Bank, and Nantucket Shoals during the autumns and winters of 1976–77, 1988–89, 1989–90, 1990–91, 1991–92, 1992–93, and 1993–94 (Fig. 1; Table 1). The samples were collected with a continuous double-oblique haul by using a 61-cm bongo net sampler (0.505- and 0.333-mm mesh) deployed to a maximum depth of 200 m (100 m in 1976–77) or to within 5 m of the bottom in shallower areas. Further details of the sampling gear and protocols can be found in Posgay and Marak (1980) and Sibunka and Silverman (1984). Atlantic herring larvae were removed for otolith analysis immediately following the haul and preserved in 95% ethanol.

In the laboratory, larvae representative of the size-range collected were selected for analysis. Standard length was measured to the nearest 0.1 mm prior to removal of the otoliths. Differential shrinkage with respect to standard length was corrected by using Theilacker's (1980) algorithm, which was specified and discussed in Bolz and Lough (1983). The 2 sagittae and 2 lapilli were dissected from each fish and mounted whole on microscope slides with Permount. The growth increments on most of the otoliths were discernible without any further preparation.

The sagittae were viewed under a Zeiss compound microscope with transmitted light. The number of



**Figure 1**

Station locations in the Gulf of Maine–Georges Bank region where larval herring were collected for otolith ageing.

growth increments were counted from the image projected by a drawing tube onto a Hewlett-Packard graphics tablet interfaced with an HP-87 microcomputer. All counts were made at a magnification of 800 $\times$ . Three counts were made on one sagitta from each larva, and those otoliths with a repeatable increment count of >90% were used in the growth analysis. The other sagitta was counted once for comparison. Campana et al. (1987) found that detection of increments during the first 15–20 days posthatch are probably too fine to be resolved. In a previous study by Lough et al. (1982), it was found that the mean age of a 3-increment larva was approximately 22 d; consequently, a correction factor of 19 was added

to the number of increments recorded in order to establish each larva's estimated age in days from hatch (Stevenson et al., 1989; Townsend et al., 1989). Measurements of the anterior–posterior diameters (otolith length) of the sagittae and the lapilli were made to the nearest micron.

## Results

### Larval herring growth

Otoliths were dissected, mounted, and analyzed for a combined total of 1,746 larval herring. Growth with

**Table 1**

Cruise information for larval Atlantic herring, *Clupea harengus*, specimens collected for otolith analysis during the autumn–winter field season in the Nantucket Shoals–Georges Bank region.

Vessel	Cruise no.	No. of sta.	Cruise sampling dates	No. of larvae	Mean length (mm)	Mean age (d)
<b>1976–77</b>						
<i>Wieczno</i>	76–03	1	14 Oct–03 Nov	18	16.9	31.1
<i>Researcher</i>	76–01	5	27 Nov–11 Dec	90	21.5	52.0
<i>Mt. Mitchell</i>	77–01	4	13 Feb–24 Feb	48	30.3	131.1
<i>Anton Dohrn</i>	77–01	1	15 Mar–21 Mar	34	31.8	148.4
<b>1988–89</b>						
<i>Delaware II</i>	88–12	4	31 Oct–11 Nov	43	14.4	27.3
<i>Albatross IV</i>	88–11	5	29 Nov–10 Dec	34	21.8	44.5
<i>Delaware II</i>	89–01	11	05 Jan–20 Jan	77	25.4	63.2
<b>1989–90</b>						
<i>Delaware II</i>	89–07	6	06 Nov–16 Nov	117	17.3	31.5
<i>Delaware II</i>	89–09	9	27 Nov–16 Dec	159	23.4	50.5
<i>Delaware II</i>	90–01	6	04 Jan–17 Jan	106	28.0	74.8
<b>1990–91</b>						
<i>Delaware II</i>	90–12	15	30 Oct–08 Nov	112	15.9	30.9
<i>Delaware II</i>	90–14	18	29 Nov–14 Dec	102	22.2	48.8
<i>Delaware II</i>	91–01	16	04 Jan–16 Jan	100	24.3	60.7
<i>Delaware II</i>	91–03	5	17 Feb–22 Feb	100	29.7	89.1
<b>1991–92</b>						
<i>Delaware II</i>	91–11	15	04 Nov–14 Nov	87	13.5	27.1
<i>Delaware II</i>	91–13	14	04 Dec–13 Dec	85	24.8	53.9
<i>Delaware II</i>	92–01	10	06 Jan–13 Jan	96	25.8	65.5
<i>Delaware II</i>	92–02	12	29 Jan–12 Feb	96	28.6	81.2
<b>1992–93</b>						
<i>Delaware II</i>	92–12	9	26 Oct–04 Nov	74	14.1	31.0
<i>Delaware II</i>	92–14	5	01 Dec–18 Dec	50	24.9	59.0
<i>Delaware II</i>	93–01	6	05 Jan–21 Jan	101	27.7	80.5
<b>1993–94</b>						
<i>Delaware II</i>	93–12	5	02 Nov–10 Nov	50	17.0	31.7
<i>Delaware II</i>	93–14	6	30 Nov–10 Dec	50	22.1	46.9
<i>Delaware II</i>	94–01	4	06 Jan–18 Jan	50	27.7	68.6

respect to length for each of the seven field seasons studied was best described by a Gompertz-type curve. The methodology for fitting the curve is discussed in Pennington (1979). Previous uses of the Gompertz growth curve are presented in Al-hossaini et al. (1989) and Jearld et al. (1993). The Gompertz curve not only permits the calculation of growth rate but also provides mean hatching size (length at age 0) and predicted length at metamorphosis (the asymptotic limit of mean larval growth).

Analysis of the seven field seasons resulted in the following relationships, where  $L$  = standard length in mm and  $Age$  = number of days (increments plus 19) from hatch:

$$1976/77 L = 33.5381e^{-1.1055e^{-0.0197Age}} \\ [n=187, r^2=0.8965];$$

$$1988/89 L = 38.9217e^{-1.5483e^{-0.0213Age}} \\ [n=139, r^2=0.8951];$$

$$1989/90 L = 35.2189e^{-1.6232e^{-0.0271Age}} \\ [n=379, r^2=0.8914];$$

$$1990/91 L = 36.0859e^{-1.6104e^{-0.0240Age}} \\ [n=382, r^2=0.9161];$$

$$1991/92 L = 34.1978e^{-1.9677e^{-0.0320Age}} \\ [n=313, r^2=0.8540];$$

$$1992/93 L = 34.1176e^{-2.1559e^{-0.0312Age}} \\ [n=204, r^2=0.9085];$$

$$1993/94 L = 37.4796e^{-1.8986e^{-0.0276Age}} \\ [n=142, r^2=0.9435].$$

A summary of the growth parameters generated by the above equations may be found in Table 2. Plots of the Gompertz curves fitted to standard length vs. age in days are presented in Figure 2.

In order to compare the rate of growth for the seven seasons, the Gompertz curves were linearized and examined for homogeneity of slope with  $t$ -tests (Table 3; Fig. 3). With this method, three groupings were discernible: 1) the 1976–77 season; 2) the 1988–89, 1989–90, and 1990–91 seasons; and 3) the 1991–92, 1992–93, and 1993–94 seasons. Larval growth for the 1976–77 season was the slowest (0.16 mm/d) of the time series, and although larvae for this season had the greatest hatch length, standard length at 120 days posthatch was 2.2 to 4.8 mm less than that in the other six years. There was no significant difference at the 0.05 level between the 1988–89, 1989–90, and 1990–91 seasons. Hatching length for these three seasons differed by less than 1.5 mm, and overall rates of growth for the first 120 days were identical. The rate of growth during the overwintering period of 1988–89 was the greatest of the seven years

and compensated for the relatively slow growth earlier in the season. Larvae were on average 2.7 mm smaller at hatching in the autumns of 1991, 1992, and 1993 than in the preceding three years. The rate of growth for the first 40 to 60 days was considerably faster than that in previous years; however, this initial rapid increase in length was followed in 1991–92 and 1992–93 by a period of slower than average growth. The overall higher rates of growth in these two years were not enough to compensate for the small size of larvae at hatching (4.0–4.8 mm), and projected lengths at metamorphosis (34.1–34.2 mm) were smaller than in all previous years except 1976–77. Although hatching lengths in 1993–94 were small, growth was good throughout the season, and the average length at 120 days posthatch (35.0 mm) was the largest of the time series.

### Predictability

A generalized growth model for larval herring was created by pooling data ( $n=1,559$ ) from the six most recent field seasons (1988–94) and by fitting them with a Gompertz curve:

$$L = 34.9959e^{-1.7424e^{-0.0281Age}} \\ [r^2=0.8863].$$

The model tracks growth for the first four months of life from an estimated hatch length of 6.1 mm to a predicted length at 120 days posthatch of 33.0 mm (0.22 mm/d). Figure 4 shows the growth curve with 95% confidence intervals for predicting standard length (mm) for a given age in days. This information is also presented in Table 4 along with age-specific growth rates.

Because it is desirable, especially during field surveys when direct analysis of otoliths is impossible, to be able to estimate the age of larvae based on their length, inverse regression (Draper and Smith, 1966) was performed on the Atlantic herring composite growth curve to establish confidence intervals for predicting age from a given standard length. In its reduced form the equation obtained for herring was

$$\frac{X_U}{X_L} = \frac{\ln \left( \frac{1 - X_0 \pm 0.0470t}{\left( \left( (X_0 - 0.7523)^2 / 26.5957 \right) + (1 + 1/n) \right)^{1/2}} \right)}{-0.0281}$$

where  $X_U$  and  $X_L$  = upper and lower confidence limits;

$$X_0 = 1 - e^{-0.0281}; \text{ and}$$

$$n = \text{sample size.}$$

**Table 2**

Summary of larval Atlantic herring growth parameters based on otolith analysis for the autumn–winter field seasons of 1976–77, 1988–89, 1989–90, 1990–91, 1991–92, 1992–93, and 1993–94.

	1976	1988	1989	1990	1991	1992	1993
<b>Sample size</b>	187	139	379	382	313	204	142
<b>Corrected standard length (mm)</b>							
Hatching length	11.1	8.3	6.9	7.2	4.8	4.0	5.6
Inflection of lapillus	—	—	29.1	29.1	28.9	29.4	—
120 days posthatch	30.1	34.5	33.1	33.0	32.9	32.4	35.0
Metamorphosis length	33.5	38.9	35.2	36.1	34.2	34.1	37.5
<b>Growth rate (mm/d)</b>							
Age (d)							
0	0.24	0.27	0.31	0.28	0.30	0.26	0.29
20	0.23	0.30	0.35	0.32	0.41	0.39	0.38
40	0.20	0.28	0.30	0.29	0.35	0.36	0.35
60	0.16	0.23	0.22	0.23	0.23	0.26	0.26
80	0.12	0.18	0.15	0.16	0.14	0.16	0.18
100	0.09	0.13	0.09	0.11	0.08	0.09	0.11
120	0.06	0.09	0.06	0.07	0.04	0.05	0.07
<b>Overall</b>	0.16	0.22	0.22	0.22	0.23	0.24	0.24

**Table 3**

Summary statistic comparing growth curves for the seven field seasons analyzed. Values in boldface indicate no significant difference at the 5% level.

	<i>t</i> -value						
	1976–77	1988–89	1989–90	1990–91	1991–92	1992–93	1993–94
1976–77	—						
1988–89	-5.9188	—					
1989–90	-10.4849	<b>-1.7146</b>	—				
1990–91	-10.6624	<b>-1.3390</b>	<b>-0.6648</b>	—			
1991–92	-15.0114	-6.4908	-6.6106	-7.5418	—		
1992–93	-17.5134	-8.5801	-9.5920	-10.7229	-2.7409	—	
1993–94	-13.5369	-5.4810	-4.9987	-5.8684	<b>0.9600</b>	-3.5349	—

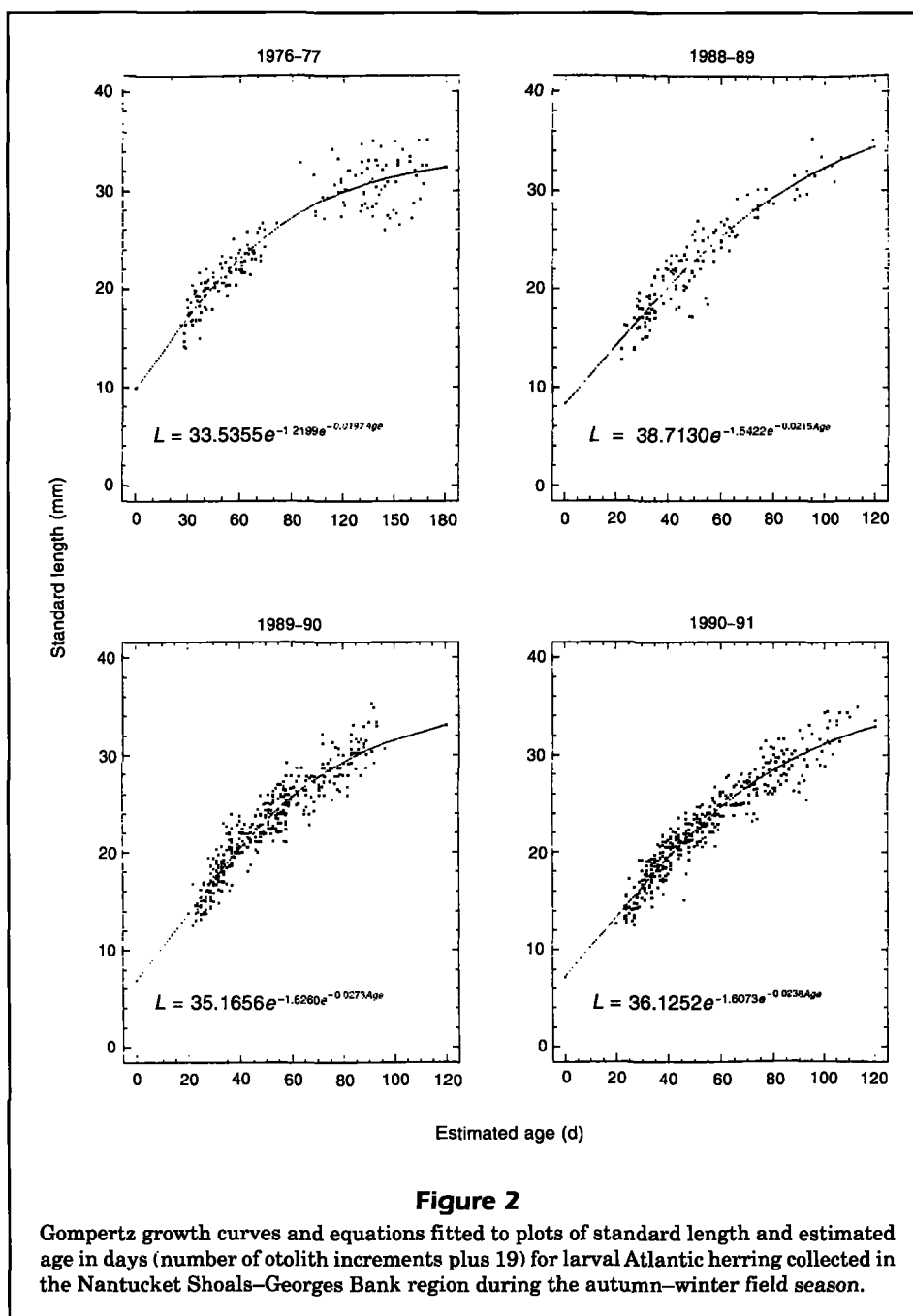
Table 5 provides predicted ages of Atlantic herring for given standard lengths with 70% and 95% confidence limits, and Figure 5 shows the fitted growth curve bracketed by its confidence limits.

### Otolith growth

Because past studies have demonstrated a strong relationship between mean otolith diameter ( $\mu\text{m}$ ) and age (d) (Bolz and Lough, 1987), sagittal growth for the seven seasons was analyzed and compared. The extremely slow growth in otolith diameter during the 1976–77 season was dramatically different from the other six years and resulted in a one-third smaller

diameter at metamorphosis (Fig. 6). During 1988–89 and 1993–94, there appeared to be a decoupling of somatic and otolith growth, such that 120-day-old larvae were approximately 1.4–2.6 mm longer than those in the four other recent field seasons and had a smaller otolith diameter.

Beginning with the 1989–90 season, the length of the lapilli, as well as that of the sagittae, was measured. A plot of diameter of the lapillus versus age in days showed an abrupt increase in its rate of growth at approximately 2.5 months of age (Fig. 7). In 1989–90 and 1990–91 the point of flexion occurred at a length of 29.1 mm SL when the larvae were 79 and 84 days old, respectively. Change in the growth of



the lapillus occurred at 77 days in 1991-92 and at 86 days in 1992-93 when the fish were respectively 28.9 and 29.4 mm SL. Owing to the small number of larger individuals sampled during the 1993-94 season, it was not feasible to determine when inflection took place.

### Discussion

With the collapse of the herring fishery in the Nantucket Shoals-Georges Bank region during the autumn of 1976, initial larval abundance dropped from

an estimated  $62.5 \times 10^{12}$  larvae in 1975 to  $2.8 \times 10^{12}$  in 1976 (Lough et al., 1985). This low abundance was further diminished by strong and persistent northerly winds that occurred during November, January, and February of the 1976-77 season (Wright, 1979; Bolz and Lough, 1984). The computed Ekman transport indices (Lough et al., 1979) are indicative of strong southerly transport. These winds with their resultant offshore surface drift would have disrupted the normal spatial distribution of prey (Maillet and Checkley, 1991).

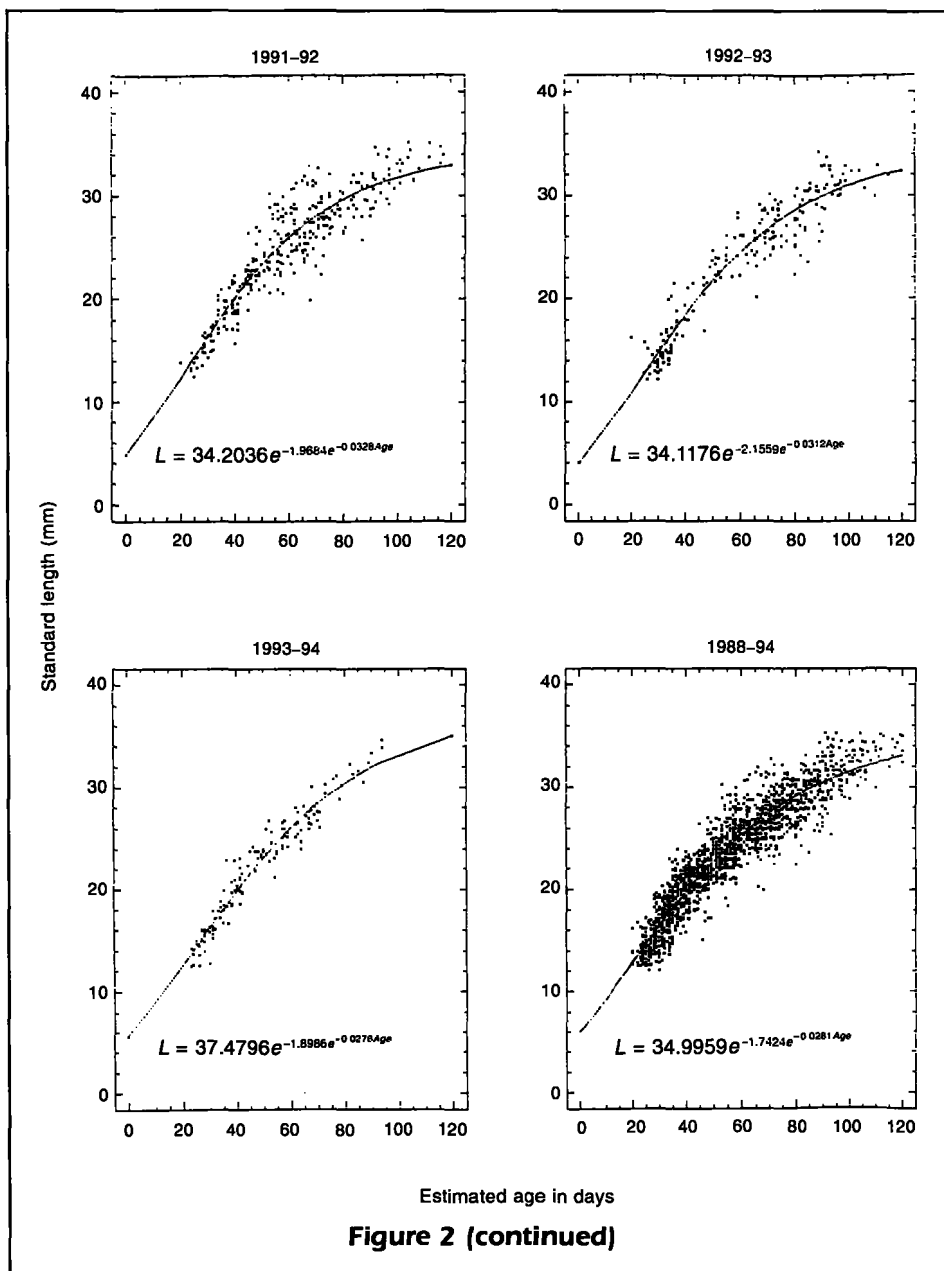
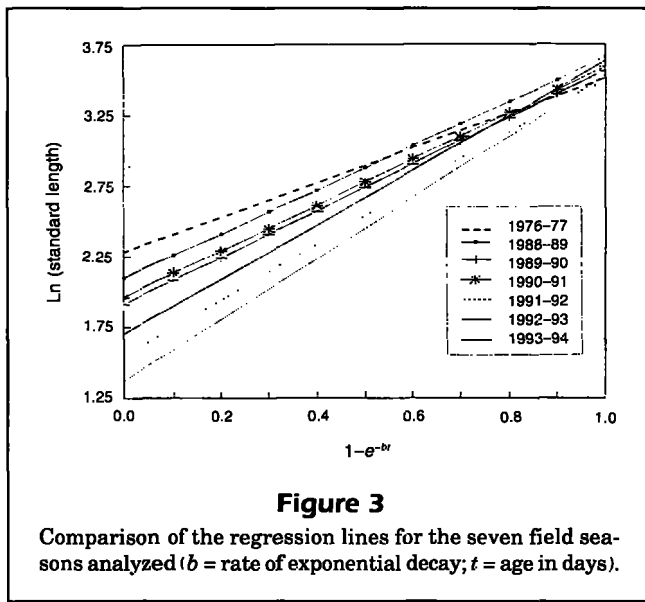


Figure 2 (continued)

Fish hatched in 1976 were longer by 2.8 to 7.1 mm SL than those collected during the 1980's and early 1990's. Since temperatures in the autumn of 1976 did not differ significantly from the long-term average (Mountain and Holzwarth, 1989), a density-dependent function is the most likely explanation for this difference. It is possible that the less dense beds enhanced growth by permitting eggs to be oxygenated better or that the diminished spawning population produced eggs with greater food reserves (Blaxter and Hunter, 1982). Despite their initially robust appearance, larvae during the 1976-77 season exhibited poor growth and high mortality (Lough

et al., 1979). The severe storms discussed above most likely dispersed the prey of larval herring and led to a reduction in daily food rations. Poor feeding is reflected in the rapid lessening of mean otolith diameter noted during 1976-77. This observation is in agreement with the previous study of Cohen and Lough (1983), where larvae collected during the 1976 season had lower prey numbers and biomass per larva than those in 1974 and 1975. Similar results were found by Karakiri et al. (1989) in their study of age-0 plaice (*Pleuronectes platessa* L.). They also concluded that food limitation accounted for an observed difference in growth between two years with similar



**Figure 3**

Comparison of the regression lines for the seven field seasons analyzed ( $b$  = rate of exponential decay;  $t$  = age in days).

temperature regimes and that the difference was likewise reflected in daily otolith increment widths.

Several studies have observed a poor correlation between otolith length and fish length (Secor et al., 1989; Moksness and Wespestad, 1989), and this was partly the case in the present work. Since increments may continue to be deposited during periods of slow or negative somatic growth, caution must be exercised in estimating age based solely on length relationships. After 120 days of growth, the fish in the 1988–89 and 1993–94 seasons showed smaller mean otolith diameters than did fish in 1989–90, 1990–91, 1991–92, and 1992–93 seasons, despite their having larger mean standard lengths. There is, however, a strong relationship between mean otolith increment width and the somatic rate of growth as expressed in mm/d of SL. From 60 to 120 days of age, larval herring grew very slowly in 1976–77 and exhibited thin increments; whereas in 1988–89, growth was more rapid and the increments were wider. Secor et al. (1989) found evidence of a lag effect between food ration and its reflection in the otoliths and, until this finding can be demonstrated in herring, it is perhaps best to cite trends rather than attempt to relate a given increment to a specific event.

The predictive model for Atlantic herring growth presented above has to be viewed as general in nature, and the widening of the confidence intervals with increasing length (Tables 4 and 5; Figs. 4 and 5) must be kept in mind. Natural variability of length at age and difficulty in the reading of otoliths increase as fish become older and make precise age determinations extremely difficult. For example, the ability to predict correctly the age of an individual herring

**Table 4**

Mean standard length at age, 95% prediction limits, and growth rate of larval Atlantic herring from hatch through 120 days, estimated from the Gompertz growth model fit.

Age (d)	Mean length (mm)	95% prediction limits		Growth rate (mm/day)
		Lower	Upper	
0	6.1	5.1	7.1	0.30
10	9.2	7.9	10.9	0.35
20	12.8	10.9	15.1	0.36
30	16.4	13.9	19.3	0.35
40	19.7	16.8	23.2	0.32
50	22.7	19.3	26.7	0.28
60	25.3	21.5	29.7	0.23
70	27.4	23.3	32.2	0.19
80	29.4	24.7	34.2	0.15
90	30.4	25.9	35.8	0.12
100	31.5	26.8	37.1	0.09
110	32.3	27.5	38.1	0.07
120	33.0	28.0	38.8	0.06

**Table 5**

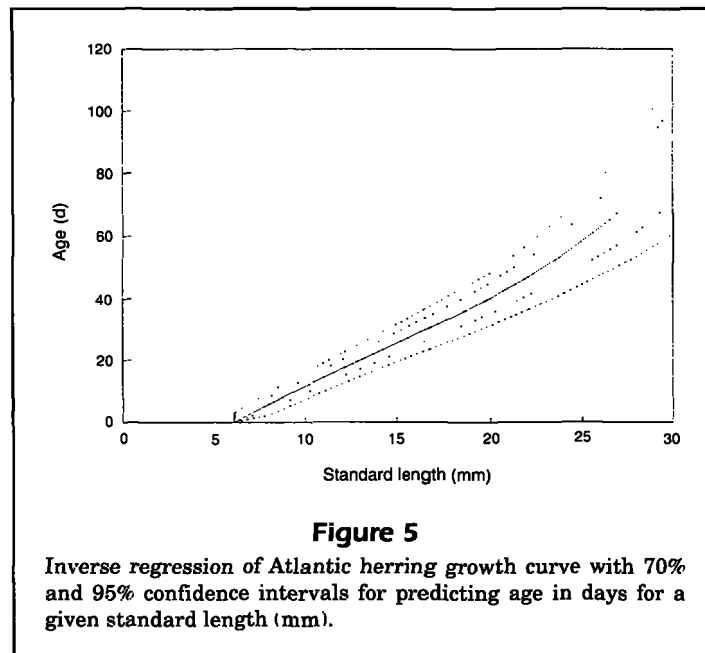
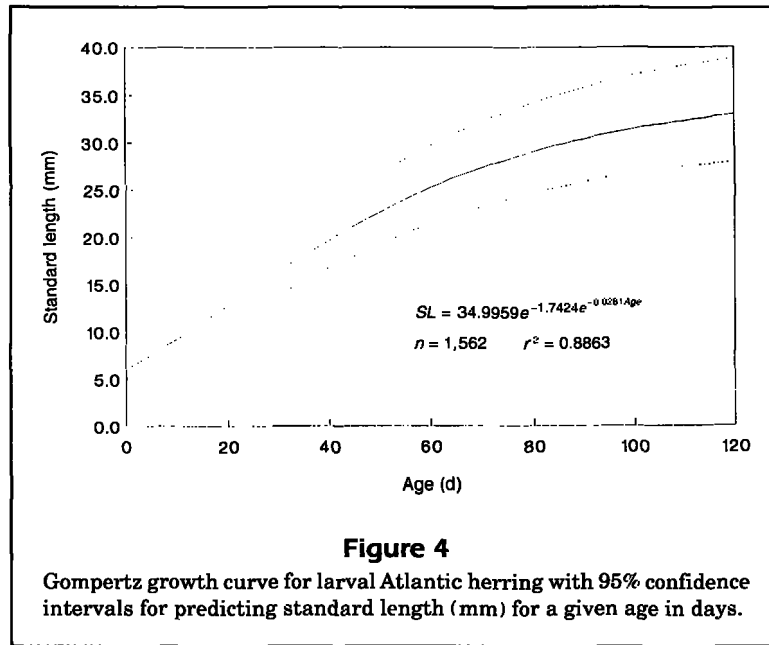
Predicted age in days, with 70% and 95% prediction limits, of larval Atlantic herring for a given standard length.

Observed standard length (mm)	Predicted age (d)	70% prediction limits		95% prediction limits	
		Lower	Upper	Lower	Upper
6.1	0	—	1.7	—	3.2
8.0	5.9	3.9	7.9	2.2	9.6
10.0	11.7	9.4	14.0	7.4	16.0
12.0	17.3	14.6	20.0	12.3	22.3
14.0	22.8	19.6	26.0	17.1	28.5
16.0	28.4	24.7	32.1	21.8	35.0
18.0	34.2	29.9	38.5	26.5	41.9
20.0	40.3	35.3	45.3	31.3	48.3
22.0	46.9	41.0	52.8	36.4	57.4
24.0	54.3	47.1	61.5	41.7	66.9
26.0	62.8	53.9	71.7	47.5	78.1
28.0	72.9	61.5	84.3	53.7	92.1
30.0	86.0	70.5	101.5	60.7	111.3

larva at the 70% confidence level decreases from  $\pm 2$  days at 8 mm SL to  $\pm 2$  weeks at 30 mm. In spite of this problem, otolith ageing of field-caught larvae provides a degree of precision not possible with indirect methods based on size-frequency analysis (Ebert, 1973).

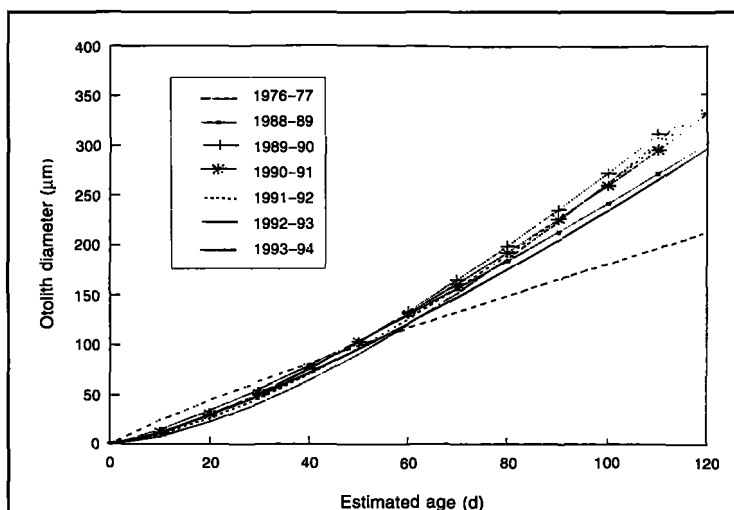
The inflection noted in the rate of otolith growth (Fig. 7) occurs at an age when the otic bullae would





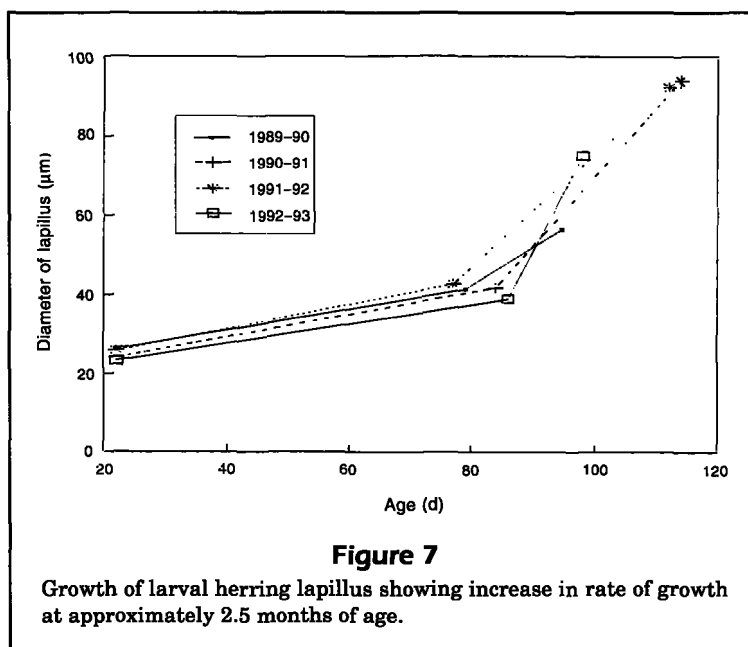
be expected to fill with air. Enlargement at this time of the lapilli and, less dramatically, of the sagittae and maculae would allow larvae to take greater advantage of the wave amplification conferred by a full air bladder and bullae. In order to successfully avoid predation and to control vertical migration, this should occur at as early an age as possible. Analysis of otolith growth is probably the only way to estimate the timing of this developmental landmark in field-caught larvae. Knowing when this occurs may

permit a better understanding of population anomalies. The necessary morphometric data are lacking for the 1976–77 season; however, from the analysis of recent seasons, the storm events in late November 1976 would be expected to have occurred while many of the larvae were at this critical life stage. This co-occurrence of storm events and critical life-stage events would have caused additional mortality to an already stressed population.



**Figure 6**

Comparison of changes in otolith growth for larval herring during the autumn-winter period of the seven years in the study.



**Figure 7**

Growth of larval herring lapillus showing increase in rate of growth at approximately 2.5 months of age.

## Literature cited

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