

GROWTH OF LARVAL ATLANTIC COD, *GADUS MORHUA*, AND HADDOCK, *MELANOGRAMMUS AEGLEFINUS*, ON GEORGES BANK, SPRING 1981¹

GEORGE R. BOLZ AND R. GREGORY LOUGH²

ABSTRACT

A study of the otoliths of larval Atlantic cod and haddock collected on Georges Bank in spring of 1981 provided information on growth and development during the first 2 months of life for these species. Exponential growth curves of length at age were fitted based on daily increment deposition which agreed with prior laboratory results and the few reported field studies. The faster growth rate (3.4% per day) of haddock larvae collected in May compared with that of cod larvae (2.6% per day) collected in April appeared to be due to the higher water temperature rather than to species-specific differences in rate of growth. Based on the microstructure of the otoliths, it was estimated that both species remained in the yolk-sac phase for 2-8 days followed by an 8-11 day period of slow growth during the transition to successful active feeding.

One of the major hypotheses of fisheries biology is that the extent of mortality during the larval phase greatly influences the size of a year class (Moser 1981). Since mortality is best described as a function of age and abundance, it is very important to be able to determine accurately the age of the larvae. Until Pannella (1971, 1974) demonstrated that the otoliths found in the semicircular canals of larval fish are composed of daily rings or increments, the only methods available for aging field-caught larvae were indirect ones based on inference, e.g., cohort analysis or growth curves generated by laboratory rearing experiments. Although the mechanisms controlling the rhythmic secretion of calcium and carbonate ions into the protein matrix of the otolith are as yet incompletely known (Watabe et al. 1982), many recent studies have demonstrated that the periodic increments formed are of a daily nature for the most part (Taubert and Coble 1977; Wilson and Larkin 1980; Schmidt and Fabrizio 1980; Tanaka et al. 1981; Mugiya et al. 1981; Townsend and Graham 1981; Rosenberg and Laroche 1982; Laroche et al. 1982; Campana and Neilson 1982; Lough et al. 1982).

In addition to containing an age record, otoliths can provide other information on the life history of larval fish (Radtke 1980; Brothers 1981; Brothers and McFarland 1981). Physiological changes or growth disturbances often are indicated on the otolith by

thick, dark bands or check rings (Radtke and Waiwood 1980; Geffen 1982). An examination of the area and the number of increments enclosed by these checks can provide insight on the duration and related environmental conditions of the early stages of larval fish. The relative width of individual increments, or small groupings of increments, provides a possible index to the daily or weekly feeding success of the larvae (Methot 1981). By knowing the precise age, hatching dates can be established and analyzed to assess yearly or population differences in the survival of larvae in relation to spawning time and location.

The work reported here was undertaken to derive accurate growth curves for larvae of Georges Bank Atlantic cod, *Gadus morhua* L., and haddock *Melanogrammus aeglefinus* L., from the field based on an analysis of their increment formation. Also, from the standpoint of understanding their larval ecology, it was important to determine what additional information might be revealed in the microstructure of cod and haddock otoliths on species differences and on stage of development in relation to environmental conditions. This study was conducted as part of the MARMAP program of the Northeast Fisheries Center, which measures long-term changes in the variability of the fish-stock abundance off the northeast coast of the United States (Sherman 1980).

METHODS

Cod and haddock larvae were collected on two larval fish dynamics cruises (Lough and Laurence 1982)

¹MARMAP Contribution MED/NEFC 82-64, Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

²Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

conducted by the Northeast Fisheries Center's RV *Albatross IV* on southeastern Georges Bank during spring 1981 (14 April-1 May-1 June). Sample dates and station location where larvae were selected for otolith analysis are shown in Figure 1 and Table 1. The samples were collected with either 1) a continuous double-oblique haul³ using a 61 cm bongo net sampler (0.505 and 0.333 mm mesh) deployed to a maximum depth of 100 m, or 2) a MOCNESS⁴ fitted with 0.333 mm mesh nets which sampled discrete vertical

³Gear configuration and other details can be found in Posgay and Marak (1980).

⁴Multiple Opening/Closing Net and Environmental Sensing System, after Wiebe et al. (1976).

layers from the bottom of the water column to the surface. Stations with high densities of cod and haddock larvae in good condition were selected during the cruises for a study of larval otoliths. Larvae were removed immediately following the haul and preserved in 95% ethanol. Temperature data for each station were obtained from surface bucket readings, expendable bathythermograph traces, or MOCNESS profiles.

In the laboratory, larvae selected for analysis were representative of the entire size-range collected. The standard length, as well as several other morphometric measurements, of each larva was measured to the nearest 0.1 mm prior to removal of their otoliths. The

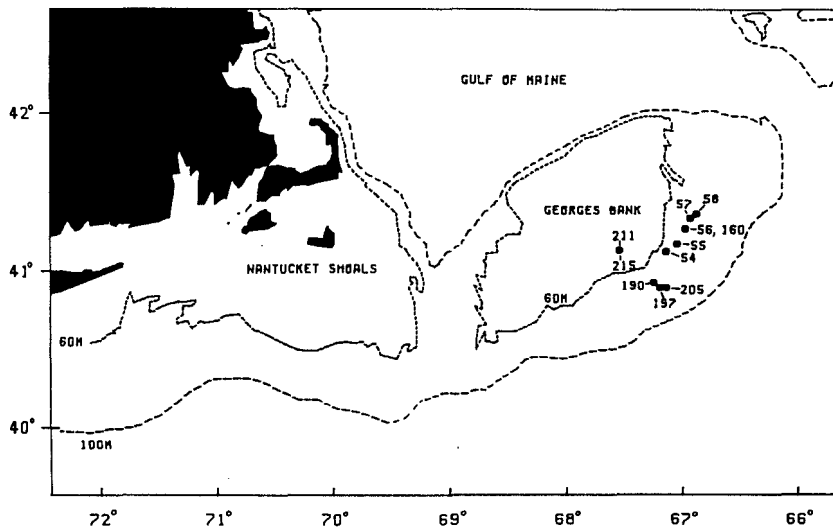


FIGURE 1.—Station locations for larval Atlantic cod and haddock specimens collected for otolith analysis aboard the RV *Albatross IV* during two cruises in the spring of 1981 (14 April-1 May; 19 May-1 June) on southeastern Georges Bank.

TABLE 1.—Station information for larval cod and haddock specimens collected for otolith analysis by 61 cm bongo net (0.505 mm mesh) oblique hauls (6B5) and 1 m MOCNESS (0.333 mm mesh) discrete vertical hauls (1M3) aboard the RV *Albatross IV* during two cruises in the spring of 1981 (14 April-1 May; 19 May-1 June) on southeastern Georges Bank.

Station	Lat. N	Long. W	Date (GMT)	Time (GMT) (Night or day)	Gear	Bottom depth (m)	Temp. (°C) at 20 m	No. larvae	Mean standard length (mm)	Mean no. otolith increments
Cod Larvae										
54	41°10'	67°06'	24 April	1235 (D)	6B5	62	5.8	19	12.4	38.2
55	41°13'	67°02'	24 April	1330 (D)	6B5	62	5.8	10	12.2	38.3
56	41°18'	66°58'	24 April	1450 (D)	6B5	66	5.7	16	11.0	32.6
57	41°22'	66°55'	24 April	1630 (D)	6B5	66	5.8	13	11.1	33.6
58	41°26'	66°51'	24 April	1840 (D)	6B5	71	5.7	12	12.6	39.5
160	41°22'	67°00'	26 April	0645 (N)	1M3	63	4.9	29	16.8	44.8
Haddock Larvae										
190	40°57'	67°19'	22 May	0300 (N)	1M3	76	6.7	8	8.4	22.4
197	40°55'	67°13'	25 May	1200 (D)	1M3	80	6.9	16	4.6	12.1
205	40°55'	67°09'	26 May	1130 (D)	1M3	80	6.8	6	5.8	12.1
211	41°11'	67°35'	27 May	1200 (D)	1M3	49	8.2	27	9.4	27.9
215	41°12'	67°36'	27 May	2330 (N)	1M3	40	8.2	19	8.1	23.2

2 sagittae, 2 lapilli, and, when possible, 2 asterisci were dissected from the larvae and mounted whole on microscope slides with Permount⁵. The growth increments on most of the otoliths were discernible without any further preparation.

The largest of the otolith pairs, the sagittae, were then viewed under a Zeiss compound microscope with transmitted light. The number of growth increments were counted from the image projected by a drawing tube onto a Zeiss MOP Digital Image Analyzer System. This method was found to be superior to the microscope-television system used in previous studies (Lough et al. 1982) in terms of both increment resolution and the time necessary for repetitive counts. Depending on the size of the otolith, magnifications used ranged from 400 \times to 1,000 \times . Three counts were made on one of the 2 sagittae from each larvae, and those otoliths with a repeatable increment count of $\geq 95\%$ were used in the growth analysis. The other sagitta was counted once for comparison.

The following measurements were made routinely

on each sagitta to the nearest micron (Fig. 2): 1) Anterior and posterior radii from the center of the otolith nucleus to the outer edge of the otolith (otolith length); 2) diameter of the sagitta perpendicular to the length (lateral diameter); 3) diameter of the nucleus; 4) diameter of that portion of the otolith deposited prior to yolk-sac absorption as defined by Radtke and Waiwood (1980); and 5) planar surface area of the entire otolith. Diameters and planar surface areas of the lapilli and asterisci also were measured.

In order to distinguish faint increments within and immediately outside of the nuclear check, several otoliths of both cod and haddock larvae were examined by using a scanning electron microscope (SEM). After securing the otoliths to a microscope slide with Clear 2-Ton epoxy, they were ground with 1 μm diamond polishing compound. The grinding procedure was monitored periodically by viewing the otolith under a compound microscope. Next, the otoliths were etched with 10% HCl for 5-15 s. The epoxy containing the ground and etched otolith was removed from the slide, attached with double-sided tape to SEM viewing stubs, and sputter-coated with gold-palladium using a Tousimis Samsputter-2A.

⁵Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

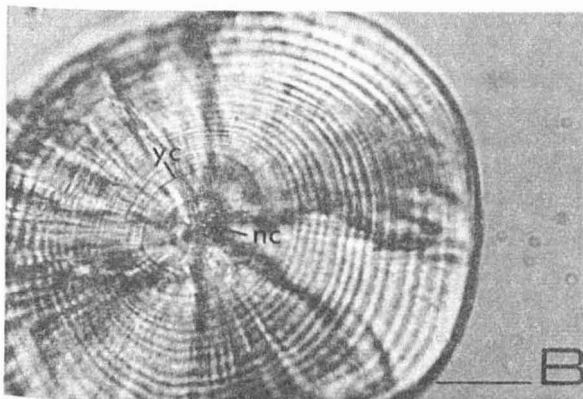
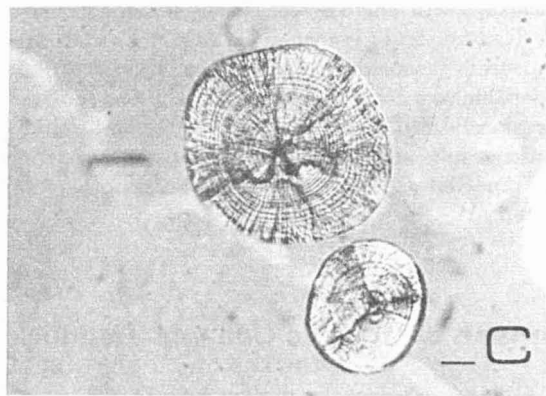
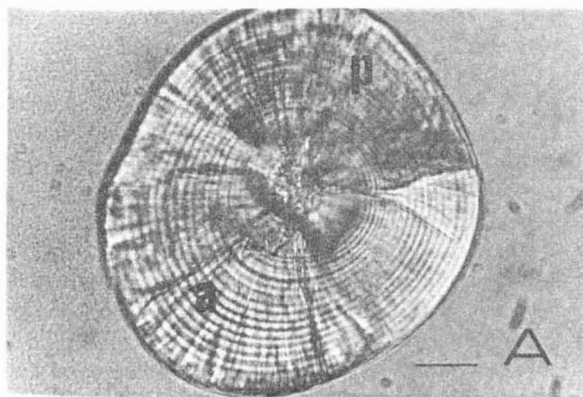


FIGURE 2.—Larval Atlantic cod and haddock otoliths. Bar of photographs represents 20 μm . a = anterior, p = posterior, nc = nuclear check, yc = yolk-sac check. A. Sagitta from 31-d-old cod larva, 12.2 mm SL (400 \times). B. Sagitta from 47-d-old cod larva, 13.3 mm SL (630 \times). Note poorly defined region enclosed by yolk-sac check followed by increments of increasing thickness towards the edge of the otolith. C. Sagitta and lapillus from 31-d-old haddock larva, 10.7 mm SL (160 \times).

The otoliths were viewed and photographed with a Semco Nanolab-7 SEM.

Radtke and Waiwood (1980) have shown that cod larvae shrink in length as much as 15% within 15 min of death and another 5% following preservation in ethanol. The amount of shrinkage was dependent on the size of the larvae. In order to correct for shrinkage, an algorithm developed by Theilacker (1980) for estimating the differential shrinkage of northern anchovy, *Engraulis mordax*, larvae with length was applied in this study to both cod and haddock larvae:

$$\ln L = \ln X_1 + 0.289e^{-0.434X_1X_2}^{-0.680}$$

- where L = standard length (mm) of the larvae prior to death and alcohol fixation;
 X_1 = standard length (mm) of the preserved specimen; and
 X_2 = length of handling time (min) from death until preservation (assumed to be about 20 min in the present study).

Although cod and haddock larvae are less fusiform in shape than northern anchovy, the percentage of shrinkage with length agrees closely with the findings of Radtke and Waiwood (1980). It therefore appeared reasonable to use Theilacker's (1980) algorithm as a correction factor for the size range of larvae collected in this study. All lengths referred to in the results and discussion portions of this paper are reported as corrected lengths unless otherwise stated.

RESULTS

Growth of Atlantic Cod and Haddock Otoliths

The inner ear of adult teleosts contains three otoliths within its membranous labyrinths: 1) The sagitta located within its sacculus; 2) the lapillus housed within the utriculus; and 3) the asteriscus situated within the lagena. When viewed under a compound microscope with transmitted light, the otoliths of cod and haddock larvae were composed of a series of light and dark rings (Fig. 2) which corresponds to the heavily calcified incremental zones and the organic-rich discontinuous zones of Watabe et al. (1982). The sagittal increments (1 incremental and 1 discontinuous zone) were segregated into three or more regions delimited by distinctly thicker, darker, discontinuous zones referred to as checks or check

rings. The innermost region or nucleus had a mean diameter of 16.2 μm (SD = 2.8) in cod and 14.7 μm (SD = 6.8) in haddock. When viewed under SEM, the nucleus was composed of a central amorphous core surrounded by a more structured area in which 1 or 2 irregular increments (Fig. 3) were discernible in some specimens. Proceeding outward from the nuclear check ring were 2-8 faint increments bounded by a discontinuous zone which appeared to be synonymous with the yolk-sac check found by Radtke and Waiwood (1980) in larval cod otoliths and with the "first heavy ring" noted by Geffen (1982) in otoliths of herring (*Clupea harengus*) and turbot (*Scophthalmus maximus*). The mean diameter of the area enclosed by the yolk-sac check was 27.2 μm (SD = 3.8) in cod and 23.5 μm (SD = 2.8) in haddock. Between the yolk-sac check and the edge of the otolith were an average of 8 (haddock) to 11 (cod) increments of $\leq 1 \mu\text{m}$ followed by thicker rings of 1-3 μm .

The sagittae and lapilli of an individual larva contained about the same number of increments, and both pairs of otoliths were present in all cod and haddock, regardless of length. In larvae < 7.0 mm SL, the sagitta and lapillus were both circular with centrally positioned nuclei and were of equal size. Cod larvae with a 10.0 mm SL had sagittae with maximum diameters 1.8 times greater than those of the lapilli, and by 25.0 mm in length the difference had further increased to 2.3 times (Fig. 4). The same trend was evident in haddock larvae, and sagittae in larvae with a 10.0 mm SL had a maximum diameter 1.5 times greater than that of the lapilli. Growth of the sagitta was relatively greater in the anterior-posterior plane, and the otolith was oval in the larger larvae. The lapillus remained roughly circular; however, deposition was not uniform and the nucleus became eccentric in larger larvae (Fig. 3).

No discernible asterisci were present in cod larvae with sagittae having > 37 increments. Extrapolation from the plot of otolith diameter vs. standard length (Fig. 4) indicated that the asteriscus first appeared when the larvae reached a length of about 9.0 mm. Once initiated, the asteriscus grew more rapidly than the lapillus and would be expected to surpass it at a length of 90 mm. No asterisci were found in the haddock larvae examined.

Atlantic Cod and Haddock Larval Growth

Figure 5 is a plot of the standard lengths (range: 7.8-24.9 mm) of 99 cod larvae vs. their number of sagittal increments (range: 13-66). Assuming that the num-

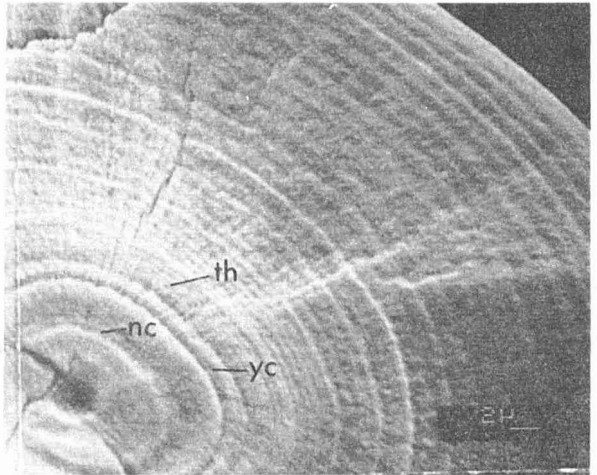


FIGURE 3.—Scanning electron micrograph of sagitta from 30-d-old haddock larva, 9.5 mm SL. Note the 1-2 poorly defined increments enclosed by the nuclear check (nc), the faint increments between the nuclear and yolk-sac (yc) check marks, and the series of very thin increments (th) immediately encircling the yolk-sac check.

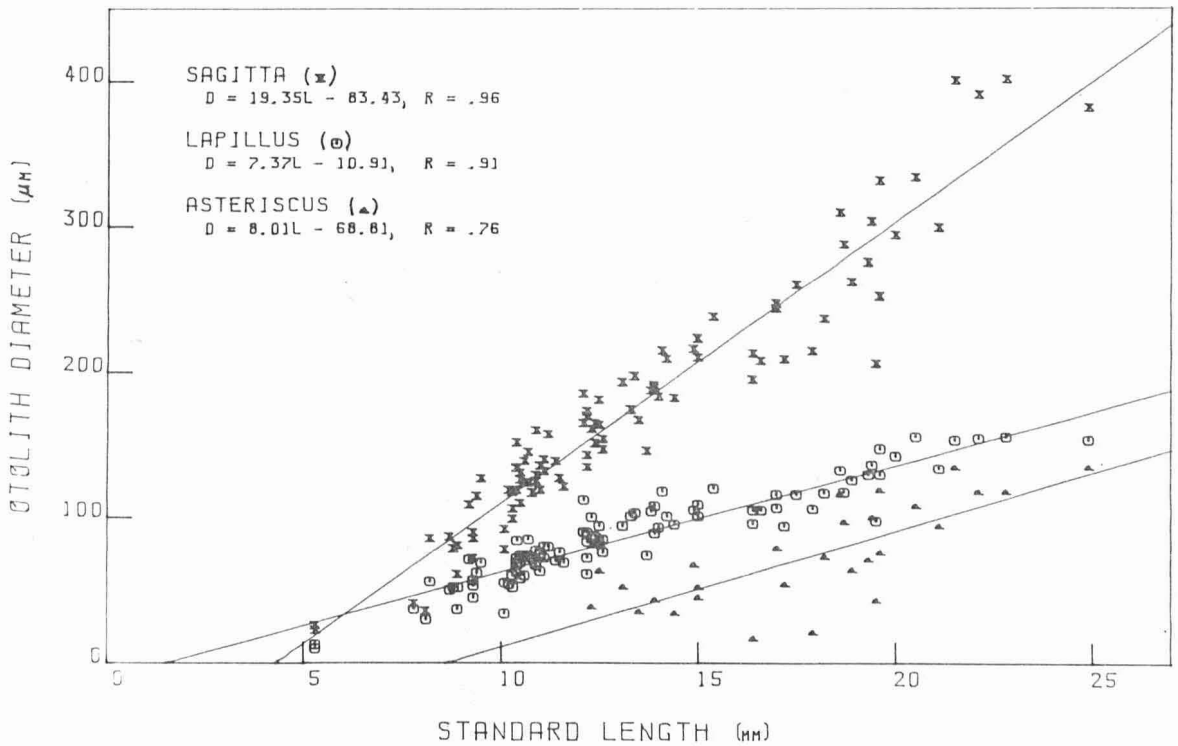


FIGURE 4.—Plot of otolith diameter:standard length fitted with linear regression lines for the three pairs of otoliths (sagitta, lapilli, and asterici) dissected from the inner ear of larval Atlantic cod.

ber of increments equals days from hatch (Radtke and Waiwood 1980; Gjösæter and Tilseth 1982), cod growth through the first 2 mo of life may best be described by the exponential relationship:

$$L = 4.82e^{0.0250R}, r = 0.92 \quad (1)$$

where L = standard length in mm, and
 R = number of days (increments) from hatch.

The average growth rate of cod larvae was 0.18 mm/d through the first month and 0.28 mm/d through 2

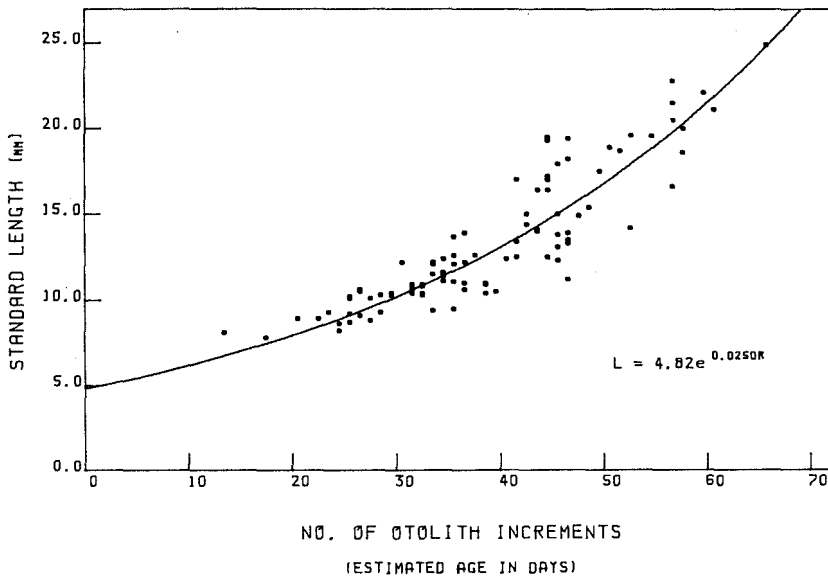


FIGURE 5.—Exponential growth curve and equation fitted to plot of standard length: no. of otolith increments (estimated age in days) for 99 Atlantic cod larvae collected during spring 1981 on southeastern Georges Bank.

mo. Growth continued exponentially from the predicted hatch length of 4.82 mm through the size range of larvae collected with no indication of a cessation in rate. Based on otolith age, hatching dates for the cod larvae analyzed extended from 19 February to 5 April (see Figure 7).

An exponential growth curve also resulted when the standard lengths (range: 3.5-12.7 mm) of 76 haddock larvae were plotted against their otolith increment counts (range: 5-36 (Fig. 6)):

$$L = 3.54e^{0.0346R}, r = 0.96. \quad (2)$$

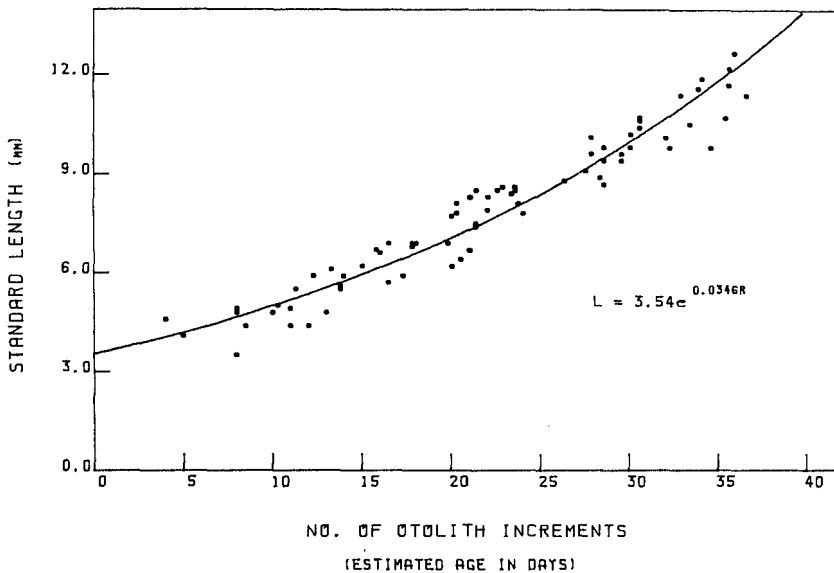


FIGURE 6.—Exponential growth curve and equation fitted to plot of standard length: no. of otolith increments (estimated age in days) for 76 haddock larvae collected during spring 1981 on southeastern Georges Bank.

As with the cod, larval haddock growth was exponential from the predicted hatch length of 3.54 mm through the size range analyzed (12.7 mm). For the first month of life, haddock grew at an average rate of 0.21 mm/d. Hatching dates for the haddock larvae occurred from 21 April to 21 May (Fig. 7).

In both cod and haddock larvae, it was not always possible to determine accurately the number of increments deposited prior to the yolk-sac check; consequently, size at hatch could be slightly less than predicted. However, since an average of only 3 increments were noted between the nuclear and yolk-sac checks in the clear otoliths, any error incurred would have little effect on the calculated growth curves.

DISCUSSION

The present work on cod and haddock concurs with the day-increment relationship found in many recent studies of fish otoliths (Mugiya et al. 1981; Tanaka et al. 1981; Uchiyama and Struhsaker 1981; Watabe et al. 1982; Lough et al. 1982). The exponential growth rates generated by the regression of standard length on otolith age (increments) agree with the findings of most previous field (Anderson 1982) and laboratory analyses of cod and haddock larvae. Length-at-age data for Southern New England cod from laboratory rearing experiments (Laurence et al. 1981) were highly correlated ($r = 0.98$) with the growth model derived for cod larvae in the present study. A 35-d-

old cod larva raised at the maximum feeding ration of 3 prey/ml had an uncorrected length of 10.75 mm which closely agrees with the estimated length from the growth curve of 10.52 mm. Gjösæter and Tilseth (1982) depict an otolith from a preserved 5.1 mm North Sea cod larva with the same number of increments (9) as predicted by the growth model. However, Steffensen's (1980) work on daily growth increments of juvenile East Baltic cod does not agree with these studies. The number of increments recorded by him are much lower for a given length than were found in the present analysis, e.g., a 60 mm fish with only 46 increments. His results should be viewed with caution, as he states that the central portion of his otoliths was blurred and "that an unknown number of growth zones in the central part of the otolith have escaped detection."

It is necessary to examine the central portion of the otolith carefully in order to establish when daily increment formation is initiated, as there is considerable variation between species (Brothers et al. 1976). The intercept values of 4.82 mm for cod and 3.54 mm for haddock derived from the growth model fall within the range of reported hatching lengths for the two species collected previously in the Gulf of Maine (Colton and Marak 1969). An intercept of 4.75 mm calculated from length-at-age data for larval and juvenile cod collected in Woods Hole, Mass., and tabulated by Bigelow and Schroeder (1953) also compared closely with the estimate for cod larvae. Brothers and McFarland (1981) noted 3 diffuse

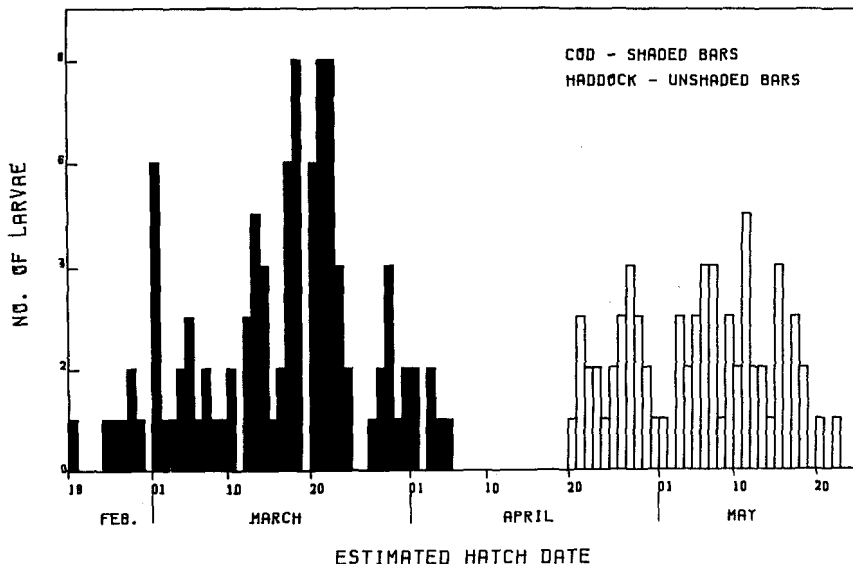


FIGURE 7.—Estimated hatch dates for Atlantic cod and haddock larvae collected during spring 1981 on southeastern Georges Bank based on otolith age (no. of daily increments).

increments in the otolith core of French grunt, *Haemulon flavolineatum*, and speculated that they may have been deposited during the egg stage, and Radtke and Dean (1982) found that laboratory-reared mummichogs, *Fundulus heteroclitus*, deposited 2 or 3 increments prior to hatching. It therefore seems reasonable to infer that the 2 or 3 irregular increments found inside the nucleus of cod otoliths by SEM analysis also were formed at some point during the approximately 20-d incubation period (Radtke and Waiwood 1980) prior to hatching. The subsequent exclusion of these innermost increments from the growth model, combined with the calculated intercept values, supports the findings of Radtke and Waiwood (1980) that cod larvae begin daily growth-ring formation at hatch. The similarity of the otoliths and growth patterns of cod and haddock warrants the conclusion that daily increment formation for haddock larvae also begins at hatch.

Checks or check rings, exceptionally dark and thick discontinuous zones, are the primary landmarks present in larval otoliths and have been used extensively to date growth disturbances, injury, poor feeding, and environmental conditions (Taubert and Coble 1977; Radtke and Waiwood 1980; Lough et al. 1982; Radtke and Dean 1982; Geffen 1982). If the discontinuous zone represents a fixed period during the day when calcium deposition into the organic matrix slows or ceases as postulated by Watabe et al. (1982), check rings would be a reflection of a disturbance in the daily metabolism of the larval fish. Change from one life history stage to another would represent one such possible disturbance. The nuclear check formed at hatching and the yolk-sac check were the two major check rings found in the otoliths of cod and haddock larvae. Radtke and Waiwood (1980) noted the presence of a check deposited at the time of yolk-sac absorption in laboratory-reared cod larvae, and they remarked on its similarity to the metamorphic checks found by Bailey et al. (1977) in capelin, *Mallotus villosus*. Although the increments deposited between the nuclear and yolk-sac checks were faint and difficult to discern with the light microscope, it was possible to make counts on the clearer specimens and by SEM techniques. The average number of increments in this zone for both cod and haddock larvae was 3 with a range of 2-8. Radtke and Waiwood (1980) found that it took cod larvae 4 d at 4°C to reach yolk-sac absorption, and in Laurence's (1978) rearing experiments cod and haddock had completed yolk-absorption by 7 d at 7°C. Ellertsen et al. (1980) found that yolk exhaustion for Arcto-Norwegian cod occurred within 8 d of hatching at 5°C and that feeding was initiated 2-4 d prior to this when

the jaw apparatus became completely functional. This close correspondence between rearing experiments and the present field study supports the proposition that the observed check was deposited at, or shortly before, the completion of yolk absorption and that the increments between it and the nuclear check approximate the number of days spent in the yolk-sac phase.

Because the early life history of the Atlantic cod and haddock larvae analyzed took place over an extended area and period of time, it is impossible to accurately know the temperatures at which hatching and larval growth occurred. However, based on the temperatures recorded during the two collecting cruises, it can be estimated that water temperature ranged from 4° to 6°C for cod and 6° to 8°C for haddock. The derived growth models estimate that cod grew in length at an average of 2.6%/d and haddock at 3.4%/d. Anderson (1982) recently found that a rise in the growth rate of cod larvae collected on the Flemish Cap "closely paralleled increasing surface water temperatures." Laboratory rearing experiments (Laurence 1978; Laurence et al. 1981) also found that growth for cod and haddock was positively correlated with temperature and that cod larvae grew in length about 0.62%/d faster at 7°C than at 5°C. If this percentage increase is incorporated into the cod growth model, the average rate of growth would be 3.2%/d, and most of the difference between the cod and haddock growth curves could be accounted for (Fig. 8). The similarity of these results agrees with that of Laurence (1978) in which he found no major differences between the growth rate of the two species at similar food levels, although haddock growth was slightly higher than cod at all temperatures.

Ring deposition appears to be endogenously controlled with the daily light-dark cycle acting as the primary triggering mechanism (Watabe et al. 1982). Environmental variables, such as temperature and day length, and feeding success are thought to be reflected in the relative width of the individual increments (Taubert and Coble 1977; Radtke 1980; Methot 1981). Since the thin otolith increments deposited immediately after the yolk-sac check ring represent a short period of time and are a constant feature throughout the extended hatching season, these thin daily increments were probably a reflection of the adjustment to active feeding rather than to an abrupt change in the environment. It is also known that the length of the yolk-sac phase and the adjustment to completely active feeding are somewhat dependent on temperature (Laurence 1978; Ellertsen et al. 1980); therefore, the greater number

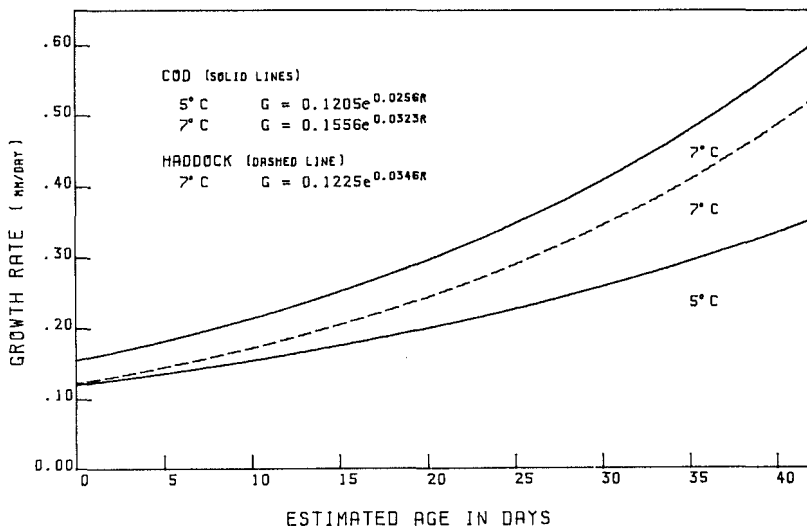


FIGURE 8.—Growth comparison of larval Atlantic cod and haddock at different temperatures. The 5°C curve for cod and the 7°C for haddock are based on an analysis of the no. of daily increments counted on otoliths from larvae collected during the spring of 1981 on southeastern Georges Bank. The 7°C curve for cod is hypothetical and incorporates the percent per day increase in growth for a 2°C temperature rise found in laboratory rearing experiments (Laurence 1978; Laurence et al. 1981).

of these thin increments found in cod (11) than in haddock (8) may have been due in part to slower growth in the cooler, late-winter water. It is also possible that the larger diameter of the yolk-sac check ring in cod (27.2 μm) than in haddock (23.5 μm) was indicative of the cod larvae having spent a longer period of time in the yolk-sac phase. However, more extensive SEM work on the region between the nuclear and yolk-sac check rings is needed to confirm the exact number of daily increments for a large sample size.

ACKNOWLEDGMENTS

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