GROWTH THROUGH THE FIRST SIX MONTHS OF ATLANTIC COD, GADUS MORHUA, AND HADDOCK, MELANOGRAMMUS AEGLEFINUS, BASED ON DAILY OTOLITH INCREMENTS[1]

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ABSTRACT

Daily growth increments of otoliths from larval and juvenile Atlantic cod and haddock were enumerated, and growth curves were derived describing the first six months of life. Growth for both species was best described by Gompertz-type curves. Inverse regressive methods were employed to construct general models with confidence limits for predicting age (days) for given standard lengths (mm) from hatching through the juvenile period. Microstructural analysis of the otoliths did not discern a settling check at the time when the fish would be expected to leave the pelagic lifestyle for the demersal one, which indicates that the transition is neither physiologically stressful nor abrupt.

Fluctuations in the year-class strength of fish stocks are thought to be determined by the rate of mortality during the first year of life (Moser 1981; Lough et al. 1985; Neilson and Geen 1986; and others). Calculation of reliable mortality rates, assessment of the influences of size-selectivity, and establishment of precise hatching dates and times during a given year when loss to recruitment is greatest are dependent upon accurate age and abundance estimates. Recently, investigators have suggested that mortality during the postlarval and juvenile periods may be as critical as that occurring in the egg and larval life stages (Cohen and Grosslein 1982; Sissenwine 1984). Investigation of this hypothesis by the Northeast Fisheries Center (NEFC) has been ongoing since 1984. Enumeration of daily growth increments deposited on fish otoliths provides the best method for the age determination of larvae and juveniles needed for generating growth curves and estimating mortality (Essig and Cole 1986). An excellent review of past and current methodologies employed in the study and application of otolith microstructure may be found in Campana and Neilson (1985).

Atlantic cod and haddock are both spring spawners on Georges Bank (Sherman et al. 1984) and have pelagic eggs and larvae that undergo similar development. Transformation to the juvenile life stage occurs around 20–30 mm SL, or 2–3 months from hatching (Fahay 1983). The transition from the pelagic to demersal habitat of the adults takes place sometime after transformation, usually by 6–8 cm in midsummer, and recent field observations by the NEFC indicates the transition is a gradual process with considerable variability.

In an earlier study by Bolz and Lough (1983), growth curves were developed for larval Atlantic cod and haddock based on otolith analysis that defined growth from hatching (4–5 mm SL) through the first two months of life (ca. 20 mm SL). Juvenile Georges Bank Atlantic cod and haddock are not fully vulnerable to bottom-trawl gear (Clark et al. 1982), and growth curves based on groundfish surveys conducted by the NEFC in the autumn and spring are inaccurate for fish younger than about six months of age. The primary goal of the work reported here was to derive age-at-length curves for field-caught Atlantic cod and haddock describing their growth from hatch until they are fully available to capture by bottom-trawl survey gear. A secondary objective was to determine if a check ring, a wide incremental band indicative of physiological or environmental changes, was deposited during the juvenile's transition from the pelagic to the demersal mode of life.

METHODS

Atlantic cod and haddock larvae and juveniles were collected on six cruises conducted by the NEFC's RV *Albatross IV* and RV *Delaware II* on

Georges Bank during the springs of 1981, 1983, and 1984 and the summers of 1984 and 1985. Sample dates and station locations where larvae and juveniles were collected for otolith analysis are given in Table 1. The samples were collected with either 1) a continuous double-oblique haul using a 61 cm bongo net sampler (0.505 and 0.333 mm mesh) deployed to a maximum depth of 100 m (Posgay and Marak 1980), 2) a 1 m MOCNESS[3] fitted with nine 0.333 mm mesh nets which sampled discrete vertical strata from the bottom of the water column to the surface, 3) a 10 m MOCNESS (3 mm mesh) with five nets fished in the same manner as the 1 m MOCNESS (Wiebe et al. 1976, 1985), or 4) a Yankee 36 otter trawl towed for 30 minutes (Grosslein 1974). Stations with

high densities of Atlantic cod and haddock larvae and juveniles in good condition were selected during the cruises for otolith analysis. The fish were removed immediately following the haul and preserved in 95% ethanol.

In the laboratory, larvae and juveniles representative of the entire size-range collected were selected for analysis. The standard length, as well as several other morphometric measurements of each larva or juvenile, was measured to the nearest 0.1 mm prior to removal of their otoliths. The 2 sagittae, 2 lapilli, and, when possible, 2 asterisci were dissected from the fish and, excepting juvenile sagittae, mounted whole on microscope slides with Permount[4]. The growth increments (Fig. 1A) on most of these otoliths were

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[3]Multiple Opening/Closing Net and Environmental Sensing System.

[4]References to trade names do not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Station information for Atlantic cod and haddock specimens collected for otolith analysis by 61 cm bongo net (0.505 mm mesh) oblique hauls (6B5), 1 m MOCNESS (0.333 mm mesh) discrete vertical hauls (1M3), 10 m MOCNESS (3.0 mm mesh) discrete vertical hauls (10M), and Yankee 36 otter trawl (Y36) during the 1981, 1983, and 1984 survey seasons.

Station	Lat. N	Long. W	Date	Time GMT (Night or day)	Gear	Bottom depth (m)	Number of fish Cod	Number of fish Haddock
1981	*Albatross IV* 81–03							
54	41°10′	67°06′	24 April	1235(D)	6B5	62	19	—
55	41°13′	67°02′	24 April	1330(D)	6B5	62	10	—
56	41°18′	66°58′	24 April	1450(D)	6B5	66	16	—
57	41°22′	66°55′	24 April	1630(D)	6B5	66	13	—
58	41°26′	66°51′	24 April	1840(D)	6B5	71	12	—
160	41°22′	67°00′	26 April	0645(N)	1M3	63	32	—
1981	*Albatross IV* 81–05							
190	40°57′	67°19′	22 May	0300(N)	1M3	76	—	8
197	40°55′	67°13′	25 May	1200(D)	1M3	80	—	16
205	40°55′	67°09′	26 May	1130(D)	1M3	80	—	6
211	41°11′	67°35′	27 May	1200(D)	1M3	49	—	27
215	41°12′	67°36′	27 May	2330(D)	1M3	40	—	19
1983	*Albatross IV* 83–03							
415	40°54′	67°32′	13 May	1816(D)	1M3	74	7	2
418	40°56′	67°35′	14 May	0456(D)	1M3	71	11	16
421	40°51′	67°34′	14 May	1026(D)	1M3	68	2	13
432	40°47′	67°26′	15 May	1636(D)	1M3	89	1	—
434	40°46′	67°24′	15 May	2229(D)	1M3	93	2	—
438	41°05′	67°47′	16 May	1147(N)	1M3	54	—	15
440	41°09′	67°54′	16 May	1646(N)	1M3	52	3	3
442	41°08′	67°48′	16 May	2222(N)	1M3	40	10	—
444	41°09′	67°55′	17 May	0504(N)	1M3	52	13	—
1984	*Albatross IV* 84–05							
519	41°19′	67°19′	18 June	0319(N)	10M	47	—	30
1984	*Delaware II* 84–07							
76	40°53′	66°22′	15 Aug.	1744(D)	Y36	66	1	1
85	41°50	66°26′	16 Aug.	1045(D)	Y36	78	—	1
88	41°49′	66°23′	16 Aug.	1430(D)	Y36	62	—	1
89	41°47°	66°18′	16 Aug.	1604(D)	Y36	68	—	4
90	41°47′	66°24′	16 Aug.	1715(D)	Y36	78	—	3
91	41°47′	66°30′	16 Aug.	1821(D)	Y36	72	—	1
93	41°45′	66°30′	16 Aug.	2024(D)	Y36	75	—	1
94	41°42′	66°25′	16 Aug.	2124(D)	Y36	75	—	1
98	41°47′	66°11′	17 Aug.	0249(N)	Y36	70	4	—
1984	*Albatross IV* 84–09							
18	41°49′	66°16′	12 Sept.	0845(N)	Y36	70	—	9
19	41°52′	66°21′	12 Sept.	0951(N)	Y36	90	1	12
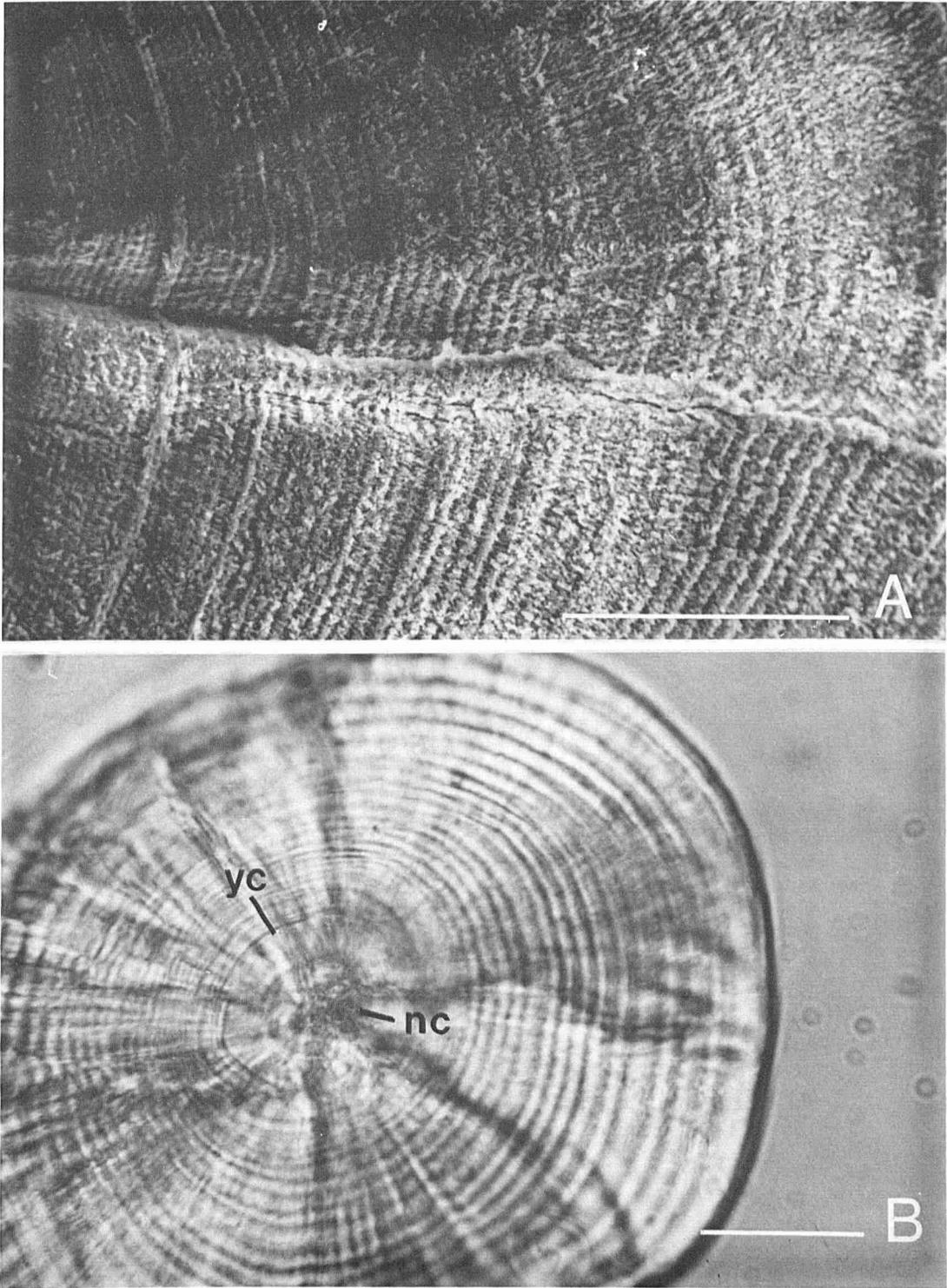
FIGURE 1.—A. Scanning electron micrograph for a portion of the sagitta from a 5-yr-old Atlantic cod, 79 cm SL, showing daily growth increments. Bar of photograph represents 100 μm. B. Sagitta from 47-d-old Atlantic cod larva, 13.3 mm SL (630×). Bar of photograph represents 20 μm. nc = nuclear check, yc = yolk-sac check.

discernible without any further preparation. Sagittae from fish >25 mm SL were mounted in epoxy resin and were ground, above and below, with carborundum paper (600 grit). The resulting thin section was secured to a microscope slide with epoxy resin and etched with 6% EDTA (pH 7.0). Both the grinding and etching procedures were monitored periodically by viewing the sagitta under a dissecting microscope.

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. Under transmitted light each growth increment was composed of a light and dark ring (Fig. 1B), which corresponded to the heavily calcified incremental zone and the organic-rich discontinuous zone of Watabe et al. (1982). Depending on the size of the otolith, magnifications used ranged from 400× to 1,000×. Three counts were made on one of the 2 sagittae from each larva or juvenile, and those otoliths with a repeatable increment count of >90% were used in the growth analysis. The other sagitta was counted once for comparison, as were the 2 lapilli. The number of increments on the 2 asterisci also were enumerated. It was found in the previous study (Bolz and Lough 1983) that the asterisci were not detectable at hatching, in contrast to the sagittae and lapilli, but appeared later in the larval period. This was reflected in the asterisci having on average 27 fewer growth increments than the sagittae. In those instances where the sagittae and lapilli were particularly difficult to read, the number of asteriscal increments plus 27 was consulted as an additional check. Maximum and minimum diameters and planar surface area of the entire otolith were measured routinely on all sagittae, lapilli, and asterisci.

The differential shrinkage of Atlantic cod and haddock larvae and juveniles with respect to standard length was corrected using Theilacker's algorithm (1980), which is specified and discussed in Bolz and Lough (1983). All lengths referred to in the results and discussion portions of this paper are reported as corrected lengths.

RESULTS

Haddock Larval and Juvenile Growth

From analysis of the 189 larval and juvenile haddock, ranging from 3.5 to 123.4 mm SL, we found that growth was best described by a Gompertz-type curve. Previous uses of the Gompertz growth curve and methodology for fitting the curve are described in Pennington (1979), Lough et al. (1982), and Messieh et al. (1987). The variance was stabilized by using the natural log form of the growth equation, and parameters were derived by nonlinear estimation techniques resulting in the relationship:

$$\ln(L) = 1.1987 + 4.8438(1 - e^{-0.0088R}), \quad (1)$$

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

A plot of the Gompertz curve fitted to the natural log of standard length vs. age in days is shown in Figure 2.

The predicted hatch-length from the curve of 3.32 mm falls within the range of previous studies (Colton and Marak 1969; Fahay 1983). An average growth rate of 0.24 mm/day (Table 2) for the first 30 days is also reasonable (Laurence 1978; Laurence et al. 1981) and agrees with the earlier study of Bolz and Lough (1983). As a generalized model the Gompertz equation described haddock growth through the first six months (175 days), at which point it intersected (Fig. 3) the von Bertalanffy growth curve generated from an analysis of adult haddock by Clark et al. (1982):

TABLE 2.—Mean standard length at age, 95% confidence limits, and growth rate (mm/day and %/day) of larval and juvenile haddock from hatch through 200 days estimated from the Gompertz growth model fit.

Age (d)	Mean length (mm)	95% confidence limits		Growth rate (mm/day)	Growth rate (%/day)
		Lower	Upper		
0	3.32	3.22	3.41	0.14	4.22
10	4.99	4.88	5.11	0.20	4.01
20	7.27	7.13	7.41	0.26	3.58
30	10.25	10.07	10.42	0.34	3.32
40	14.03	13.80	14.26	0.42	2.99
50	18.70	18.39	19.02	0.51	2.78
60	24.34	23.89	24.80	0.61	2.55
70	30.98	30.34	31.63	0.71	2.32
80	38.63	37.74	39.53	0.82	2.12
90	47.27	46.08	48.51	0.91	1.95
100	56.88	55.30	58.50	1.01	1.77
110	67.37	65.35	69.45	1.09	1.63
120	78.67	76.14	81.28	1.17	1.49
130	90.66	87.56	93.86	1.23	1.35
140	103.23	99.52	107.08	1.28	1.23
150	116.26	111.88	120.81	1.32	1.14
160	129.63	124.54	134.92	1.35	1.04
170	143.21	137.38	149.28	1.36	0.95
180	156.88	150.29	163.76	1.37	0.87
190	170.54	163.17	178.25	1.36	0.80
200	184.09	175.92	192.63	1.35	0.73
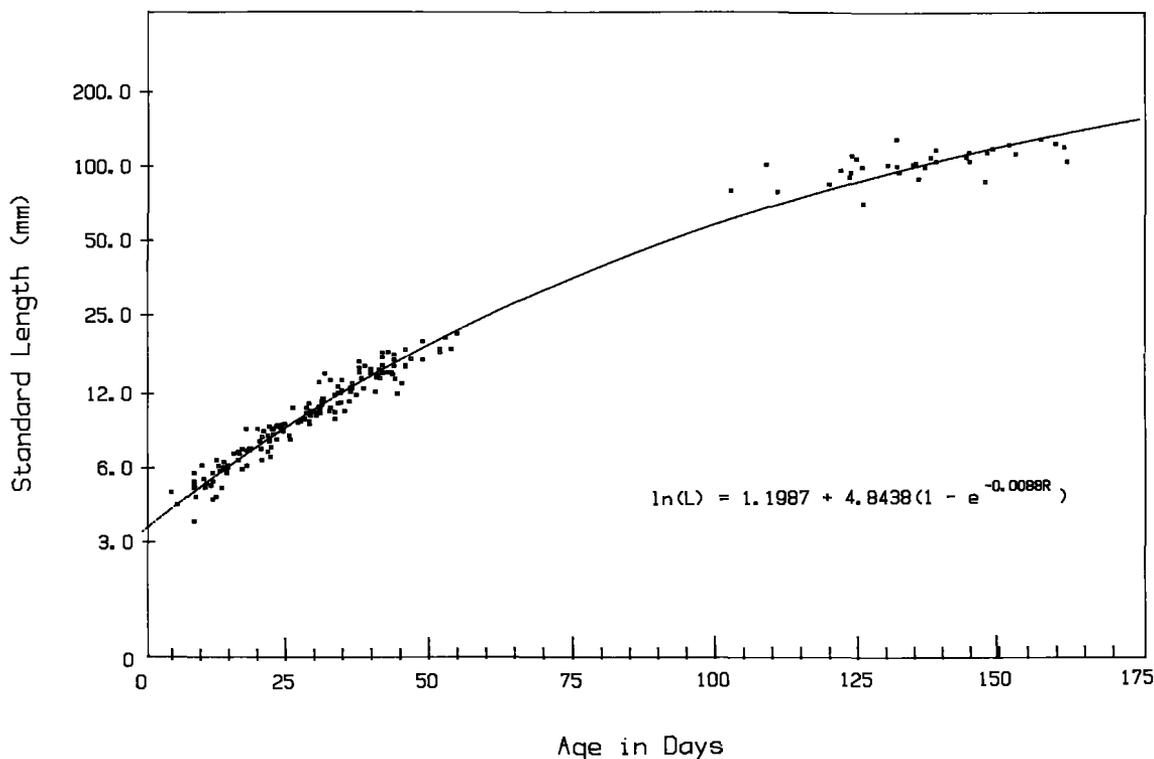
FIGURE 2.—Gompertz growth curve and equation fitted to plot of ln standard length and number of otolith increments (estimated age in days) for 189 larval and juvenile haddock collected on Georges Bank.

$$L = 738.0(1 - e^{-0.3763[(R+D)/365-0.1649]}), \quad (2)$$

where D = Julian date of hatch.

Based on the 1981 season, an average hatch-date of 15 April ($D = 105$) was employed in the present model. An average length of 19.9 cm would have been attained on 1 January, by fisheries science convention the date at which an individual is considered to be 1-year-old.

Atlantic Cod Larval and Juvenile Growth

Although there were few larger individuals amongst the 157 larval and juvenile Atlantic cod examined, the apparent pattern was similar to that seen in haddock. A Gompertz growth curve also provided a good fit when the natural log of standard length (range: 4.6–104 mm) was plotted (Fig. 4) against age in days (range: 7–151):

$$\ln(L) = 1.3915 + 6.2707(1 - e^{-0.0053R}). \quad (3)$$

The predicted hatch-length of 4.02 mm was within known limits (Colton and Marak 1969). The average growth rate of 0.21 mm/day (Table 3) through the first month was slightly lower than that of haddock, which is consistent with previous findings (Bolz and Lough 1983). At approximately 192 days the larval and juvenile growth curve intersected the von Bertalanffy curve calculated for adult Atlantic cod by Penttila and Gifford (1976):

$$L = 1481.0(1 - e^{-0.1200((R+D)/365-0.6160)}). \quad (4)$$

For purposes of the model a mean hatch-date of 15 March ($D = 74$) was assumed. An average Atlantic cod would be expected to have achieved a length of 26.1 cm by 1 January (Fig. 5).

Predictability

Since it is desirable, especially during field surveys when direct analysis of otoliths is impossible, to be able to predict age from a given length,

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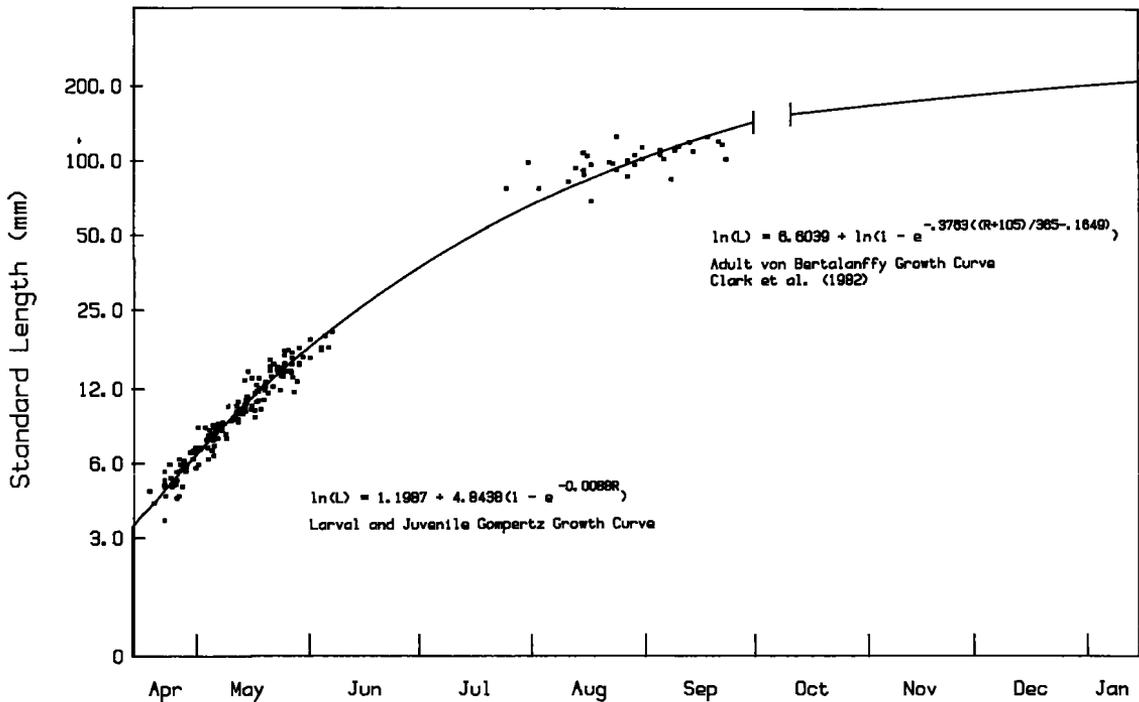
FIGURE 3.—Haddock growth model with an assumed mean hatch-date of 15 April projected through mid-January. An average length of 19.9 cm would have been attained on 01 January, by fisheries science convention the date at which an individual is considered to be 1-year-old.

inverse regression (Draper and Smith 1966) was performed on the Atlantic cod and haddock growth curves to establish confidence intervals for predicting age from a given standard length. In its reduced form the equation obtained for haddock was

$$\left.\begin{matrix}X_u \\ X_l\end{matrix}\right] = \frac{\ln(1 - (X_0 \pm 0.023t(((X_0 - 0.2990)^2/7.7959) + (1 + 1/n))^{1/2}))}{-0.0088} \quad (5)$$

where X_u and X_l = upper and lower confidence limits,
$X_0 = 1 - e^{-0.0088R}$, and
n = sample size.

Figure 6 shows the fitted growth curve bracketed by 95% confidence intervals.

Performing the same calculations on the Atlantic cod growth curve yielded the relationship:

$$\left.\begin{matrix}X_u \\ X_l\end{matrix}\right] = \frac{\ln(1 - (X_0 \pm 0.022t(((X_0 - 0.1918)^2/0.9294) + (1 + 1/n))^{1/2}))}{-0.0053} \quad (6)$$

where $X_0 = 1 - e^{-0.0053R}$.
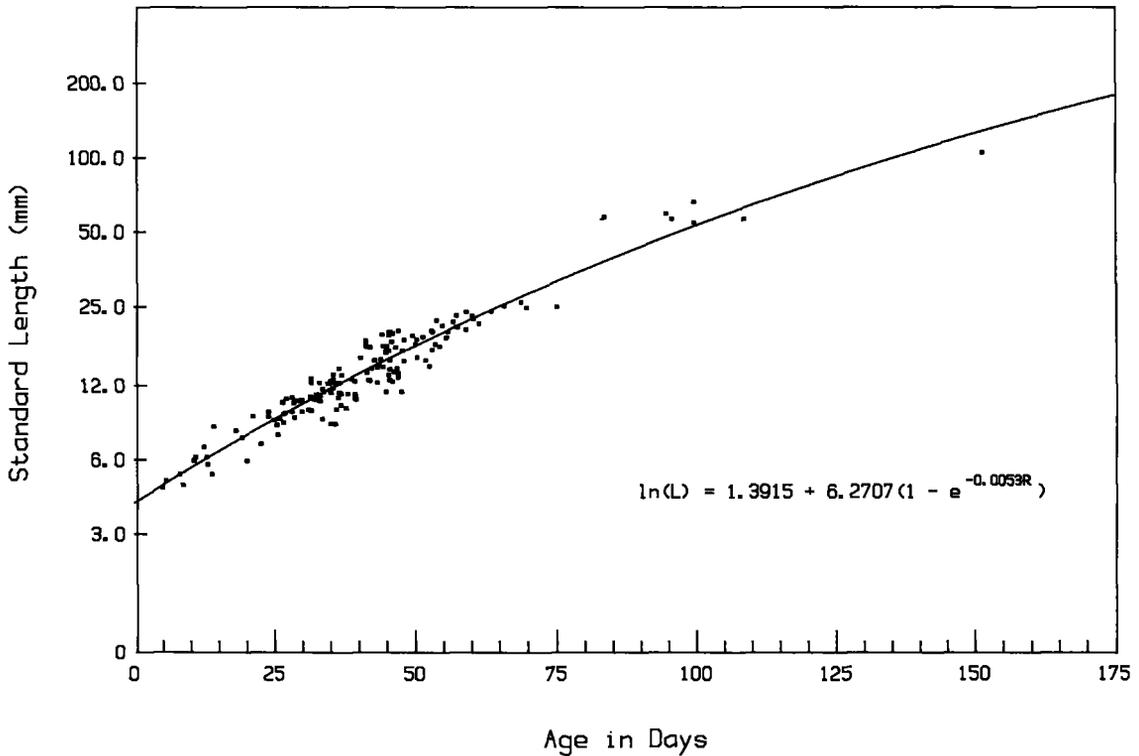
FIGURE 4.—Gompertz growth curve and equation fitted to plot of ln standard length and number of otolith increments (estimated age in days) for 157 larval and juvenile Atlantic cod collected on Georges Bank.

$$\ln(L) = 1.3915 + 6.2707(1 - e^{-0.0053R})$$

TABLE 3.—Mean standard length at age, 95% confidence limits, and growth rate (mm/day and %/day) of larval and juvenile Atlantic cod from hatch through 200 days estimated from the Gompertz growth model fit.

Age (d)	Mean length (mm)	95% confidence limits		Growth rate (mm/day)	Growth rate (%/day)
		Lower	Upper		
0	4.02	3.79	4.27	0.13	3.37
10	5.56	5.31	5.82	0.18	3.24
20	7.55	7.30	7.82	0.23	3.05
30	10.11	9.85	10.37	0.29	2.87
40	13.32	13.03	13.62	0.36	2.70
50	17.31	16.88	17.75	0.44	2.60
60	22.19	21.48	22.92	0.54	2.43
70	28.08	26.95	29.26	0.64	2.31
80	35.11	33.40	36.91	0.76	2.19
90	43.39	40.91	46.03	0.90	2.10
100	53.05	49.58	56.77	1.04	1.98
110	64.18	59.48	69.26	1.19	1.87
120	76.90	70.69	83.65	1.35	1.77
130	91.27	83.26	100.05	1.52	1.68
140	107.38	97.24	118.57	1.70	1.58
150	125.27	112.65	139.30	1.88	1.51
160	144.99	129.52	162.30	2.06	1.43
170	166.55	147.85	187.61	2.25	1.35
180	189.95	167.61	215.26	2.43	1.28
190	215.17	188.79	245.24	2.61	1.22
200	242.18	211.34	277.52	2.79	1.16

Figure 7 shows the Atlantic cod growth curve bracketed by 95% confidence intervals. Tables 4 and 5 provide predicted ages of Atlantic cod and haddock for given standard lengths with 70% and 95% confidence limits.

Otolith Growth

In the earlier study of larval Atlantic cod and haddock (Bolz and Lough 1983), it was found that the sagittal rings (one incremental and one discontinuous zone) were segregated into distinct regions separated by thicker, darker discontinuous zones referred to as checks or check rings. Two "heavy rings" were noted in the larvae: 1) a nuclear check surrounding a central, amorphous core and 1 or 2 irregular rings, and 2) a yolk-sac check 2–8 increments farther outward (Fig. 1B). The present study corroborated the existence of these two checks. Although each otolith was carefully examined for the presence of a settling check, no regularly occurring heavy ring could be discerned beyond the yolk-sac check in either the haddock or the Atlantic cod juveniles. It should,

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$$\ln(L) = 7.6822 + \ln(1 - e^{-.1200((R+74)/365+.6180)})$$
Adult von Bertalanffy Growth Curve
Penttila and Gifford (1976)

$$\ln(L) = 1.3915 + 8.2707(1 - e^{-0.0053R})$$
Larval and Juvenile Gompertz Growth Curve
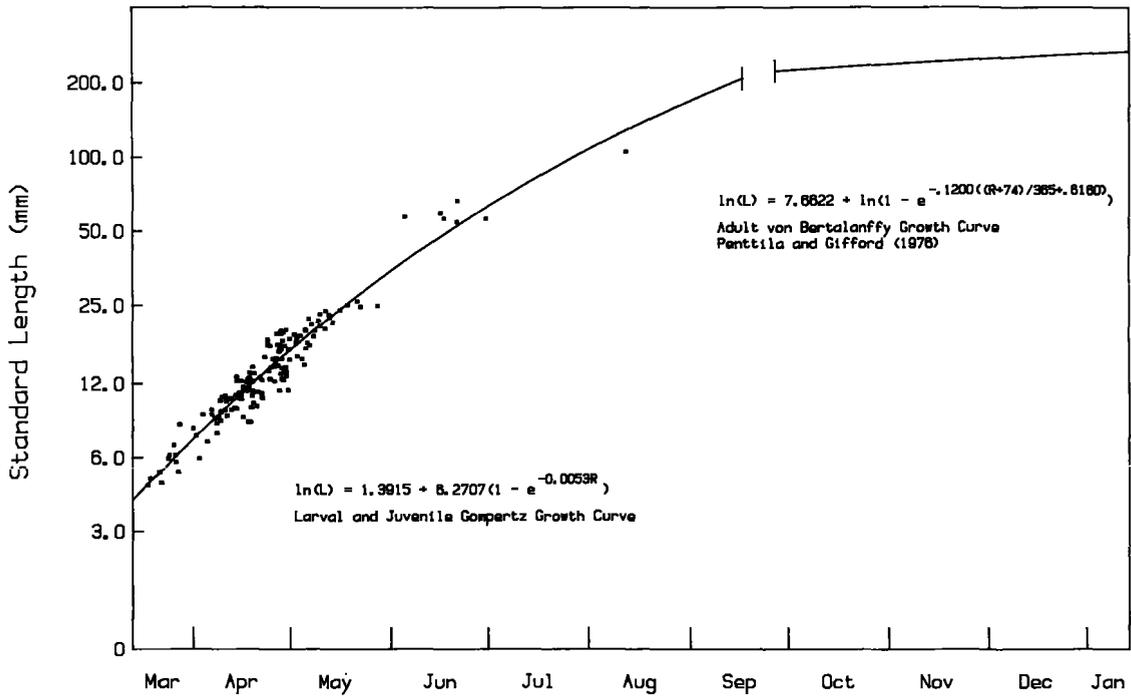
FIGURE 5.—Atlantic cod growth model with assumed mean hatch-date of 15 March projected through mid-January. An average length of 26.1 cm would have been attained by 01 January, by fisheries science convention the date at which an individual is considered to be 1-year-old.
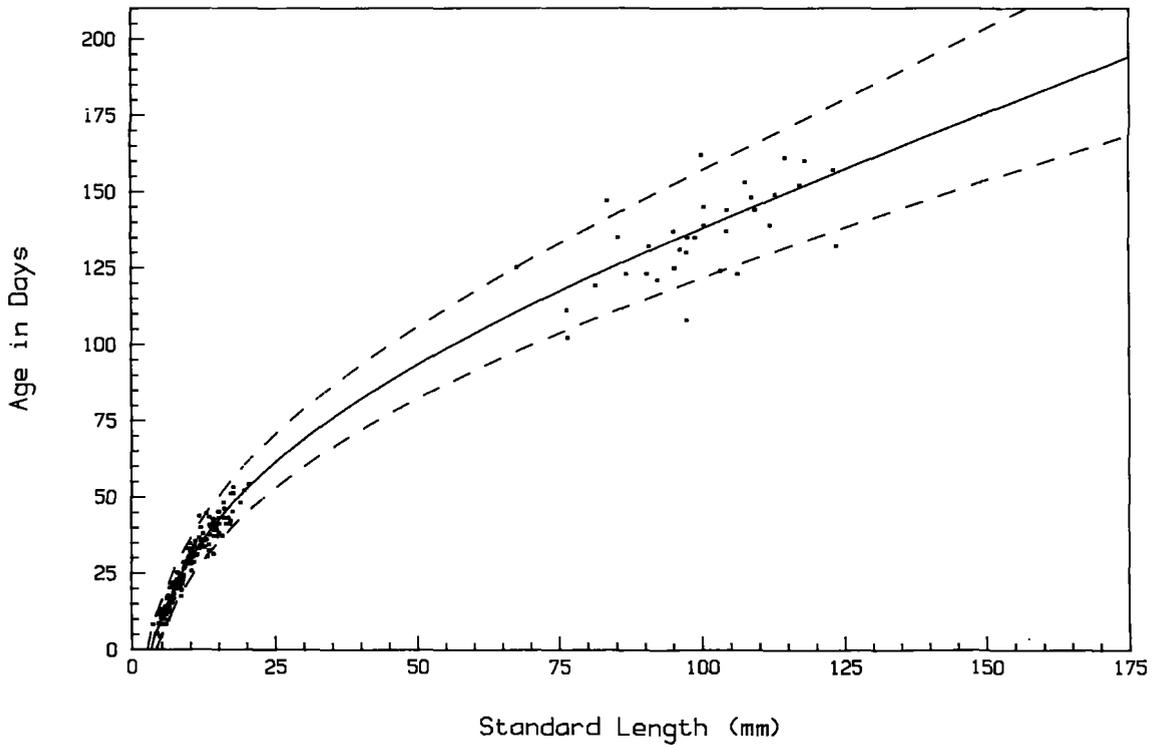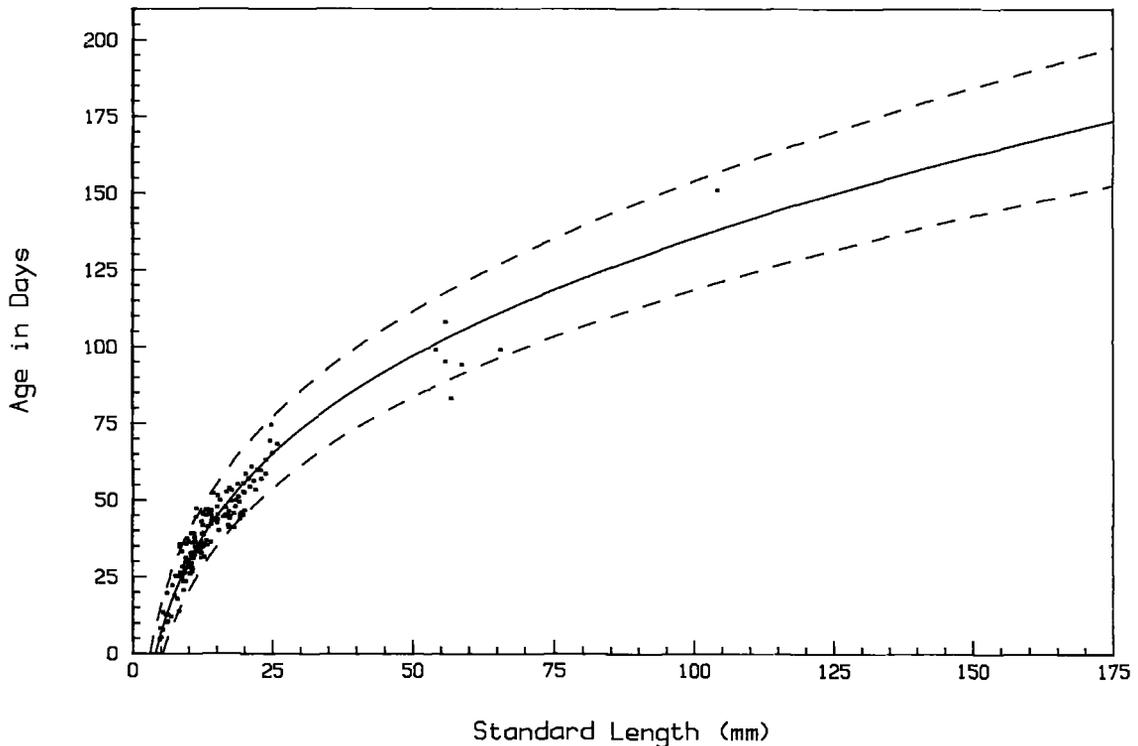
FIGURE 7.—Inverse regression of Atlantic cod growth curve with 95% confidence intervals for predicting age in days for a given standard length (mm).

however, be noted that the size range available for study limited the search for a settling check to individuals >90 mm SL and does not preclude the possibility that thinner, less discernible checks may be found when greater numbers of juveniles 50–90 mm SL are analyzed.

In both haddock and Atlantic cod diametral growth (μm) of the sagittae, lapilli, and asterisci was linearly related to standard length (mm) throughout the larval and juvenile periods. The high correlation ($r > 0.98$) of this relationship and its good agreement with measurements made by Bergstad (1984) would allow the sagittal diameter to be used as a check on the predictability model outlined in Equations (5) and (6) for estimating age from standard length. Estimated ages for haddock larvae and juveniles based on maxi-

mum otolith diameters may be obtained with the following equation:

$$Y = 28.390 + 2.413X_1 + 21.561X_2 + 73.841X_3 \tag{7}$$

where Y = estimated age in days,
X_1 = sagittal diameter in mm,
X_2 = lapillus diameter in mm, and
X_3 = astericus diameter in mm.

Table 6 provides a comparison of estimated ages derived from otolith diameters with observed ages derived from the number of daily increments. Although multiple regression analysis using the three otolith diameters yielded a high correlation coefficient ($r = 0.9890$) and nonsignificant t-values, the 95% confidence limits are quite broad (±2 weeks) and should be used with caution. Use of the sagittal diameter alone ($Y = 35.945 + 18.484X_1$) provided a good fit ($r = 0.9861$) for juveniles >90 mm SL but was a poor age predictor for younger fish. If only the sagitta is available for analysis, the relationship:

FIGURE 6.—Inverse regression of haddock growth curve with 95% confidence intervals for predicting age in days for a given standard length (mm).

TABLE 4.—Predicted age in days with 70% and 95% confidence limits of larval and juvenile haddock for a given standard length.

Observed standard length (mm)	Predicted age (d)	70% confidence limits		95% confidence limits	
		Lower	Upper	Lower	Upper
5	10.0	7.1	13.0	4.4	15.9
10	29.3	25.8	32.8	22.7	36.2
15	42.3	38.4	46.3	34.9	50.1
20	52.5	48.2	56.9	44.4	61.1
25	61.1	56.5	65.8	52.4	70.4
30	68.6	63.8	73.7	59.4	78.7
35	75.4	70.3	80.8	65.7	86.1
40	81.7	76.2	87.4	71.4	93.0
45	87.5	81.7	93.5	76.7	99.5
50	92.9	86.9	99.3	81.6	105.6
55	98.1	91.8	104.8	86.3	111.4
60	103.1	96.5	110.0	90.7	117.0
65	107.8	101.0	115.1	95.0	122.4
70	112.4	105.3	120.0	99.0	127.6
75	116.8	109.4	124.8	103.0	132.7
80	121.1	113.5	129.4	106.8	137.7
85	125.3	117.4	133.9	110.4	142.6
90	129.5	121.2	138.4	114.0	147.4
95	133.5	124.9	142.8	117.5	152.2
100	137.5	128.6	147.1	121.0	156.9
105	141.4	132.2	151.4	124.3	161.6
110	145.2	135.8	155.6	127.6	166.2
115	149.0	139.3	159.8	130.9	170.8
120	152.8	142.7	163.9	134.1	175.4
125	156.6	146.1	168.1	137.2	180.0
130	160.3	149.5	172.2	140.4	184.6
135	164.0	152.9	176.3	143.4	189.2
140	167.6	156.2	180.4	146.5	193.9
145	171.3	159.5	184.6	149.5	198.5
150	175.0	162.8	188.7	152.5	203.2
155	178.6	166.0	192.8	155.5	207.9
160	182.3	169.3	197.0	158.5	212.7
165	185.9	172.6	201.2	161.4	217.5
170	189.6	175.8	205.4	164.3	222.4
175	193.3	179.0	209.6	167.3	227.4

TABLE 5.—Predicted age in days with 70% and 95% confidence limits of larval and juvenile Atlantic cod for a given standard length.

Observed standard length (mm)	Predicted age (d)	70% confidence limits		95% confidence limits	
		Lower	Upper	Lower	Upper
5	6.7	2.1	11.3	−2.1	15.7
10	29.6	24.5	34.8	19.9	39.8
15	44.5	39.0	50.1	34.0	55.5
20	55.8	49.9	61.8	44.7	67.6
25	65.0	58.9	71.3	53.4	77.5
30	72.9	66.5	79.6	60.8	86.0
35	79.9	73.2	86.8	67.3	93.5
40	86.1	79.2	93.3	73.1	100.3
45	91.8	84.7	99.2	78.3	106.5
50	97.0	89.7	104.7	83.2	112.2
55	101.9	94.3	109.8	87.6	117.6
60	106.4	98.7	114.6	91.8	122.6
65	110.7	102.7	119.1	95.7	127.3
70	114.7	106.6	123.3	99.4	131.8
75	118.6	110.3	127.4	102.9	136.1
80	122.3	113.8	131.3	106.3	140.2
85	125.8	117.1	135.0	109.5	144.1
90	129.2	120.3	138.6	112.5	147.9
95	132.4	123.4	142.0	115.5	151.6
100	135.6	126.4	145.4	118.3	155.1
105	138.6	129.2	148.6	121.0	158.6
110	141.5	132.0	151.7	123.7	161.9
115	144.4	134.7	154.8	126.3	165.1
120	147.2	137.3	157.7	128.7	168.3
125	149.9	139.9	160.6	131.1	171.3
130	152.5	142.3	163.4	133.5	174.3
135	155.1	144.8	166.1	135.8	177.3
140	157.6	147.1	168.8	138.0	180.2
145	160.0	149.4	171.4	140.2	183.0
150	162.4	151.6	174.0	142.3	185.7
155	164.8	153.8	176.5	144.4	188.5
160	167.1	156.0	179.0	146.4	191.1
165	169.3	158.1	181.4	148.4	193.7
170	171.5	160.2	183.8	150.4	196.3
175	173.7	162.2	186.2	152.3	198.8

$$Y = 11.875 + 112.654X_1, \quad r = 0.9129 \qquad (8)$$

should be used for the larval and postlarval period.

The equation for the estimated ages of larval and juvenile Atlantic cod (Table 7) is as follows:

$$Y = 48.202 + 8.628X_1 - 121.908X_2 + 139.733X_3,$$

$$r = 0.9292. \qquad (9)$$

When using only the sagittal diameter, the following relationship should be applied to larvae and postlarvae:

$$Y = 19.364 + 89.560X_1, \quad r = 0.8659. \qquad (10)$$

Unlike the tedious laboratory methods needed for the enumeration of otolith increments, gross measurements on a limited number of juvenile otoliths could be performed at sea.

DISCUSSION

Despite the tedious methodology required for enumerating daily growth increments in larval and juvenile otoliths, the present work suggests that it is feasible to construct age-length keys for Atlantic cod and haddock similar to those commonly applied in adult population studies (Clark et al. 1982). The value of such growth data is based on several assumptions, however. Since all conclusions drawn depend upon it, reasonable assurance of the day-increment relationship in the species being investigated is critical (Beamish and McFarlane 1987; Geffen 1987). Confidence in the growth models generated here for Atlantic cod and haddock may be found in the following inferences: 1) the predicted hatch lengths of 3.32 mm for haddock and 4.02 mm for Atlantic cod fall within known limits; 2) a high correlation for the length-at-age data with the rearing experiments of Laurence et al. (1981); and 3) the smooth-

TABLE 6.—Estimated age in days based on otolith diameters with 95% confidence limits for larval and juvenile haddock compared with observed age derived from number of daily increments.

Observed age (d)	Estimated age (d)	95% confidence limits	
		Lower	Upper
0.0	1.5	−12.3	15.4
10.0	11.3	−2.5	25.1
20.0	21.1	7.4	34.9
30.0	30.9	17.2	44.6
40.0	40.7	27.0	54.4
50.0	50.5	36.8	64.2
60.0	60.3	46.7	73.9
70.0	70.1	56.5	83.7
80.0	79.9	66.2	93.6
90.0	89.7	76.0	103.3
100.0	99.5	85.8	113.1
110.0	109.3	95.6	122.9
120.0	119.0	105.3	132.8
130.0	128.8	115.1	142.6
140.0	138.6	124.8	152.5
150.0	148.4	134.5	162.3
160.0	158.2	144.3	172.2
170.0	168.0	154.0	182.0
180.0	177.8	163.7	191.9

TABLE 7.—Estimated age in days based on otolith diameters with 95% confidence limits for larval and juvenile Atlantic cod compared with observed age derived from number of daily increments.

Observed age (d)	Estimated age (d)	95% confidence limits	
		Lower	Upper
0.0	7.1	−6.9	21.1
10.0	15.8	2.1	29.5
20.0	24.5	11.0	38.0
30.0	33.2	19.9	46.5
40.0	41.9	28.7	55.1
50.0	50.6	37.5	63.8
60.0	59.3	46.2	72.5
70.0	68.0	54.8	81.2
80.0	76.7	63.4	90.1
90.0	85.4	71.9	98.9
100.0	94.1	80.4	107.9
110.0	102.8	88.8	116.9
120.0	111.6	97.2	125.9
130.0	120.3	105.5	135.0
140.0	129.0	113.8	144.1
150.0	137.7	122.1	153.3
160.0	146.4	130.3	162.5
170.0	155.1	138.5	171.7
180.0	163.8	146.6	180.9

ness with which the larval and juvenile curves flow into those independently developed for the adults (Clark et al. 1982; Penttila and Gifford 1976).

The predictive models for Atlantic cod and haddock have to be viewed as general in nature, and the widening of the confidence intervals with increasing length (Tables 4, 5) must be kept in mind. Natural variability of length-at-age and difficulty in the preparation and reading of otoliths increases as the fish becomes older and makes precise age determinations extremely difficult. For example, the ability to predict correctly the age of an individual haddock at the 70% confidence level decreases from ±3 days at 5 mm SL to ±2 weeks at 175 mm. In spite of this problem, otolith aging of field-caught larvae and juveniles provides a degree of precision not possible with indirect methods based on size-frequency analyses (Ebert 1973). Refinement of the estimated means and the reduction and stabilization of the variance should result as a greater number of otoliths are analyzed in the future.

Microstructural examination of larval Atlantic cod and haddock otoliths clearly delineated check rings related to hatching and yolk-sac absorption (Bolz and Lough 1983). Both of these transitions are abrupt, and the dark, thick discontinuous zones readily observable on the otoliths are a reflection of metabolic disturbances undergone at these times. Although additional check rings were noted in 3 or 4 of the juvenile otoliths, there was no regularity with respect to age of their occurrence. In these individuals the checks were probably the result of physiological trauma induced by disease or injury since calcium carbonate secretion ceases not only with the metabolic changes accompanying transitional phases but during times of stress (Morales-Nin 1987). It was suspected that a distinct check, similar to the settling check found by Victor (1982) in the bluehead wrasse, *Thalassoma bifasciatum*, would be found demarcating the transition from the pelagic to the demersal mode of life with its accompanying changes in diet and activity levels. No check rings were found in the transition period (50–100 days) on the otoliths analyzed. This suggests that an abrupt metabolic disturbance does not occur at this phase of the fish's life and that settling near the bottom takes place over an extended period of time (1–2 months) even for individual fish. This agrees with a preliminary finding for Scotian Shelf gadoids by Campana and Neilson (1985). However, in a recent study by Mahon and Neilson (1987) on the gut contents of Scotian Shelf haddock, they concluded that the transition from pelagic to demersal life occurred relatively suddenly, less that a month for the individual fish. Apparently, change to the demersal life stage is not stressful for Atlantic cod and haddock, at least as a metabolic manifestation recorded in their otoliths.

When used in conjunction with length-frequency data collected throughout the year, the Atlantic cod and haddock growth curves presented in this report should allow accurate estimates of the following: 1) peak hatching dates, 2) the number of cohorts produced within a given season, 3) intraseasonal changes in growth and mortality rates of cohorts, and 4) which part of the spawning curve the recruits originated from (Methot 1983). In the future year-to-year comparison of deviations in these estimates could lead to the construction of viable recruitment models permitting the early prediction of year-class strength.

ACKNOWLEDGMENTS

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