Age validation and growth of larval and juvenile haddock, *Melanogrammus aeglefinus*, and pollock, *Pollachius virens*, on the Scotian Shelf

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Abstract.–Daily growth increments on otoliths were used to estimate the age of larval and juvenile haddock, *Melanogrammus aeglefinus*, and pollock, *Pollachius virens*, collected on Emerald and Sable Island Banks, eastern Canada, between March 1991 and May 1993. The daily periodicity of the increments was validated from observations of reared larvae. For both species, the first increment was deposited the day after hatching and thereafter one increment was added daily. A Laird-Gompertz growth curve was fitted to length–age data for each species. Growth rates in haddock and pollock larvae varied significantly in different years. For haddock, the lowest growth rate was for the 1993 cohort, and growth rates in 1991 and 1992 cohorts were similar. For pollock, the 1993 cohort had the highest growth rate. The average growth rate was 0.21 mm/d for the first month and 0.42 mm/d for the second month for larval haddock and 0.18 mm/d for the first month and 0.23 mm/d for the second month for larval pollock. Growth continued exponentially after the transition from a primarily pelagic life to a predominantly demersal one, which occurred at an age of about 40–50 d. No indication of a cessation in growth was observed. Analysis of length–age data indicated that the accelerated growth of juveniles after 50 d in age could have reflected the exploitation of a more abundant food resource after settlement. Thus, pelagic and early demersal growth appear to represent distinct stanzas in the growth history of these gadoids.

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A central problem in fisheries research is understanding mechanisms determining year-class strength. Growth, which is considered critical to the survival and subsequent recruitment of larval marine fishes (Houde, 1987), is likely strongly affected by temperature and food availability (Ricker, 1979). Food limitation can affect survival directly by causing starvation (Lasker, 1975) or indirectly by retarding growth rate which in turn increases mortality from predators (Rothschild and Rooth, 1982). In addition, feeding conditions may change markedly owing to density independent factors, such as temperature, which can directly affect growth rates (Laurence, 1978).

Ware (1975) suggested that growth and mortality rates interact to determine survival of fish populations. A prediction of this hypothesis is that predation is a major factor affecting year-class strength and that mortality due to predation is inversely related to growth rate (Ware, 1975; Shepherd and Cushing, 1980). This hypothesis assumes that average growth is below the maximum and that feeding conditions that maximize growth are associated with minimal mortality.

Calculation of reliable rates of growth and mortality of larval fish, and determination of when loss due to recruitment is greatest, requires accurate determinations of age. Accuracy and precision of growth estimates for larval fishes have been greatly enhanced by the discovery of daily growth increments on otoliths (Pannella, 1971; reviewed by Campana and Neilson, 1985). Ageing by counting otolith growth increments, along with measurements of the width of the increments, provides a means of estimating the relation between length at age. In this way, growth curves, and even individual growth rates, have been calculated for a variety of species (Brothers et al., 1976; Struhsaker and Uchiyama, 1976; Taubert and Coble, 1977; Radtke and Waiwood, 1980).

Daily increments have been shown to occur in most species, nevertheless validation of the frequency of increment deposition is required before larval age can be estimated from otolith measurements. To validate increment deposition, Geffen (1987) recommended sampling reared larvae throughout the larval stage. This approach had previously been used for a number of species, for example, to determine when the first increment is deposited in Atlantic cod (*Gadus morhua*) larvae (Radtke and Waiwood, 1980) and to validate the daily increment formation in Pacific herring (*Clupea pallasi*) (Moksness and Wespestad, 1989). In the present study, I vali-

dated whether increments are deposited daily in haddock otoliths (*Melanogrammus aeglefinus*) using the same approach. Preliminary results on larval pollock (*Pollachius virens*) are also presented. Finally, daily increment analyses are used to estimate age and growth rates of larval and juvenile haddock (*M. aeglefinus)* and pollock (*P. virens)* from the Emerald and Sable Island Banks on the Scotian Shelf off eastern Canada.

Materials and methods

Study area and collection of larvae

The Scotian Shelf is a 62,000 km^2 area with an average depth of 90 m. It is bounded on the southwest by Northeast Channel entering the Gulf of Maine and on the northeast by the Laurentian Channel and Gulf of St. Lawrence. Several shallow offshore banks along the outer edge of the shelf are separated from one another by deeper channels that open onto interior basins having depths of >100 m (O'Boyle et al., 1984). The general water circulation on the Scotian Shelf is dominated by the Scotian current which flows southwesterly and parallel to the Nova Scotia coast and which carries a mixture of slope water and diluted waters from the Gulf of St. Lawrence (e.g. Sutcliffe et al., 1976; Drinkwater et al., 1979).

Eggs, larvae, and juveniles of *M. aeglefinus* and *P. virens* were collected during 20 surveys made on Emerald and Sable Island Banks (Fig. 1) from March 1991 to May 1993 (Table 1), as part of the program of Ocean Production Enhancement Network (OPEN) (Griffin and Anderson, 1993). Sampling was conducted using a grid of 45 stations (Fig. 1) with an interstation spacing of approximately 30 km. A 50-cm bongo frame with 150- and 250-µm mesh nets (March–May 1991) as well as a rectangular midwater trawl (RMT, 2–8 m^2) (Baker et al., 1973) with nets of 2 m^2 (333-µm mesh) and 8 m^2 (1600-µm mesh) were used. At each station, duplicate oblique hauls were made from near the bottom to the surface at 2.0–2.5 knots, with a retrieval time of 30 min. After the standard grid stations were sampled, the area of maximum abundance of larval fish was revisited so that 48 h of vertical sampling could be conducted with a BIONESS sampler (1 m^2) (Eastern Marine Services E-Z-Net, Dartmouth, NS) fitted with ten 333-µm mesh nets (June 1991 to May 1993). Ten discrete depths were sampled every 4 h. Deployment sampling depths were spaced at 5-m intervals, from the bottom to the surface, and fished for 5 min at 2.0–2.5 knots. Most larval haddock and pollock were sorted at sea and preserved in 95% ethanol. Temperature and salinity profiles were recorded at each station

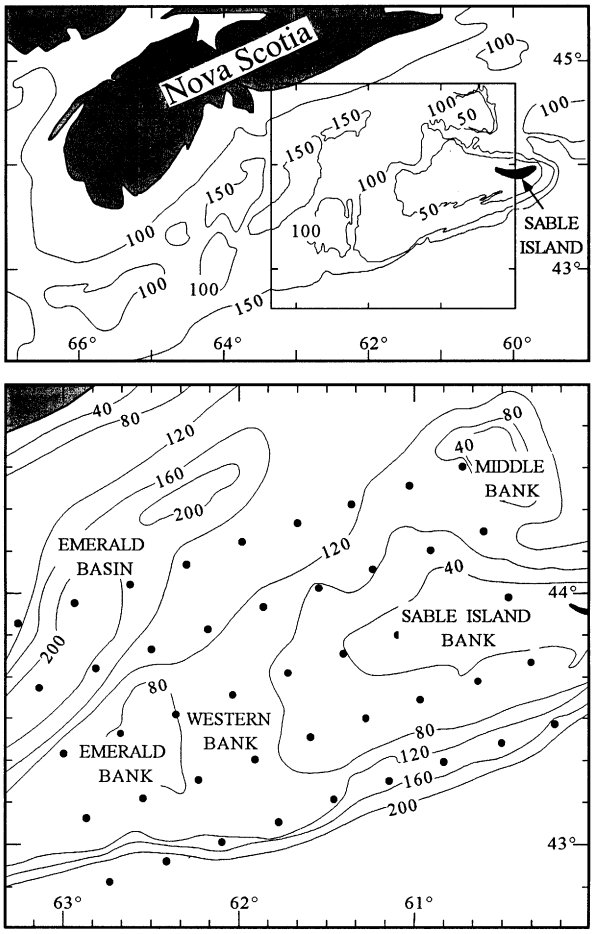

Figure 1

Study area showing stations where larval and juvenile haddock and pollock were collected on the Scotian Shelf from March 1991 to May 1993. Isobaths are in meters.

with a Sea Bird CTD probe (Sea-Bird Electronics, Inc. Bellevue, WA) connected to the electronics unit of the RMT or BIONESS sampler, or both. When the RMT or BIONESS, or both, were not used, independent CTD casts were made at each station.

A subset of pollock and haddock larvae were videotaped at sea by using a stereo dissecting microscope connected to a video camera and a magnetoscope and were then individually preserved in 95% ethanol. One to two months later, each fish was measured in the laboratory to the nearest 0.1 mm with a stereo dissecting microscope with an ocular micrometer. The unpreserved standard lengths were measured from video images recorded at sea and projected on a television monitor linked to an image analysis system. Linear regression of unpreserved standard length (SL, obtained from the videotape) to preserved standard length (PSL, after preservation in ethanol) for haddock (SL=1.531 + 1.005PSL, n=129, r^2=0.99) and pollock (SL=0.710 + 0.969PSL,

Table 1

Station information for larval and juvenile of haddock and pollock collected for otolith analysis from March 1991 to May 1993 on the Scotian Shelf. Values in parentheses are total larvae sampled.

Cruise	Vessel	Date	T (°C) at 30 m	No. of larvae examined		Mean SL of larvae (mm)		Mean no. of increments	
				Haddock	Pollock	Haddock	Pollock	Haddock	Pollock
91–01	*Petrel V*	5–11 Mar	4.0	0 (3)		3.9		—	
91–02	*Petrel V*	16–24 Apr	5.0	2 (97)		4.6		14	
91–04	*Petrel V*	17–26 May	7.0	1 (22)		7.6		23	
91–99	*Cape Keltic*	17–22 Jun	8.3	93 (164)		20.2		60	
91–08	*Petrel V*	18–27 Jul	13.5	18 (18)		60.8		105	
91–16	*Petrel V*	12–21 Nov	8.8		4 (16)		3.9		4
91–17	*Petrel V*	7–16 Dec	7.3		12 (23)		5.1		9
92–18	*Petrel V*	7–18 Jan	5.2		88 (98)		5.7		11
92–19	*Petrel V*	16–26 Feb	2.3	0 (9)	80 (218)	5.1	10.7		29
92–20	*Petrel V*	10–20 Mar	1.6	12 (66)	17 (61)	4.9	12	2	41
92–21	*Petrel V*	5–14 Apr	2.0	9 (40)	7 (33)	4.7	15	3	44
92–23	*Petrel V*	17–26 May	3.8	65 (328)	2(2)	8.1	22	21	70
92–98	*Cape Keltic*	17–22 Jun	7.3	16 (47)		22		60	
92–26	*Petrel V*	21–25 Jul	13.7	5 (5)		31.1		66	
93–32	*Petrel V*	11–22 Jan	4.0		246 (1005)		5.4		5
93–33	*Petrel V*	15–25 Feb	2.1		54 (57)		9.9		27
93–34	*Petrel V*	19–26 Mar	1.7	138 (266)	5 (5)	4.4	15.1	4	54
93–35	*Petrel V*	16–24 Apr	3.7	116 (239)	4 (4)	7.2	13.5	16	48
93–37	*Petrel V*	16–24 May	5.6	127 (290)	0 (10)	12.4	15.5	33	

n=8, r^2=0.99) were used to calculate the unpreserved standard length (SL) of fish preserved in ethanol.

Validation of ageing technique

To determine if the increments observed in otoliths of haddock and pollock were deposited daily, fertilized eggs collected in a 333 µm mesh net from the RMT were reared on the ship. Haddock eggs were collected at the Western and Emerald Banks area, February–April 1992 and 1993. Spawning begins in February around the Western Bank. Eggs were taken in the same general area on any given sampling date from February to April in both 1992 and 1993.

Some pollock eggs were collected in January–February and April 1992, as well as in October–November 1992 and January and March 1993. At the beginning of the spawning season, eggs were detected at the southeast of Sable Island Bank. In January–February the eggs were collected on the Western Bank, and in March–April the distribution of eggs included Emerald Bank. The spawning of pollock and haddock overlapped during February–April because the eggs of the two species were found together.

Immediately after the nets were brought aboard the vessel, the most advanced stages of eggs were sorted and individually placed in 20-mm vials filled with seawater which had been passed through 1-µm Hytrex filters. At this time it was impossible to distinguish between the eggs of the two species (Brander and Hurley, 1992). They were reared at 4°C in a conventional refrigerator on the ship. The photoperiod was kept at 12:12 h with dim blue light. As each egg was monitored twice daily to establish when hatching occurred, the maximum error in hatching time determinations was 12 h. After hatching, 136 zero to eleven-day haddock larvae, and nine zero to four-day pollock larvae were killed and preserved in 95% ethanol. Twelve additional 0–2 d old haddock larvae (collected on April 1993) were obtained from Flodevigen Marine Research Station, in Arendal, Norway. A total of 148 haddock larvae and 9 pollock larvae were used to examine increment formation. Because haddock and pollock eggs were indistinguishable; individuals were later identified by their larval characteristics.

Otolith preparation

A dissecting microscope illuminated with polarized light was used to dissect the sagittae and lapilli from larval skulls with the aid of fine needles. One thousand two hundred and sixty pairs of haddock and

pollock larval otoliths from the validation experiment and from wild fish <36 mm SL were mounted on glass over slides with Permount (Fisher Scientific Laboratory, Fair Lawn, NJ). Eighteen pairs of haddock otoliths from larvae measuring 50–83 mm SL were mounted with synthetic resin on metal stubs for SEM observation.

The mounted otoliths (sagittae) used in the validation experiment were read with an image analyzer system by using Optimas software (Subtechnique, Inc., Alexandria, VA). Otoliths from field-collected larvae and juveniles were read at the Southwest Fisheries Center (La Jolla, CA) by using the OTO program (Andersen and Mokness, 1988). The image analyzer system consisted of a video camera attached to a compound microscope, monitor, digitizer, and microcomputer. A detailed description of the OTO program, otolith analyzing system, and methods used are given by Andersen and Moksness (1988). Otoliths examined with SEM were ground on the sagittal plane to the nucleus with fine grit paper (between 30 µm and 0.3 µm), and then the polished surface was etched for 6 min in 0.2M EDTA (pH 7.6).

In addition to the number of increments, the following otolith measurements were taken and used in comparisons of each species: maximum otolith diameter (OD); maximum otolith radius from the center of the nucleus to the outer edge of the otolith (OR); diameter of the otolith nucleus (ON); and diameter of the yolksac resorption check (YSC) as defined by Radtke and Waiwood (1980) and Bolz and Lough (1983). Growth increments were counted twice by the same reader at an interval of 3 mo between readings. The two counts usually differed <6%, and the average was used as an estimate of age.

Statistical procedures

For both species, of all otolith measurements, the maximum otolith diameter was most strongly correlated with length. I compared the relation of otolith growth to larval growth between month and year for both species to determine whether otolith growth could be used to predict larval growth. Thus, linear regressions of LnSL on LnOD were compared by using analysis of covariance (ANCOVA) with OD as the covariate.

A Laird-Gompertz growth model curve was fitted to the length-at-age data for each species in each year. This model has been shown to provide an adequate fit for length-at-age data on age 0+ fish of many different species (Bolz and Lough, 1988; Lough et al., 1982; Watanabe et al., 1988; Simard et al., 1992). Zweifel and Lasker (1976) presented a detailed discussion of the Laird-Gompertz function. The equation for the model is

$$L_t = L_0 e^{k(1-e^{-at})},$$

where L_0 = length at t=0;
k = a dimensionless parameter, such that $ka=A_0$ is the specific growth rate at t=0 ($A_t=A_0e^{-at}$);
L_t = length at any age t;
a = the specific rate of growth when $t=t_0$; and
t_0 = the time when the growth rate starts to decrease, that is, the inflection point of the curve (Ricker, 1979).

The parameters were derived by nonlinear least squares tests by using the SYSTAT nonlinear program (Wilkinson, 1990), and ANCOVA was used to test whether differences in growth rates in different years of each species were significant.

Results

Validation of daily increment deposition

In both species, otoliths (sagittae and lapilli) were present at hatching. Some haddock otoliths (Fig. 2A) showed one to three irregular increments between the nucleus and the check at hatching, as observed by Bolz and Lough (1983). The mean (±SD) diameters of the nucleus and of the check at hatching of reared larvae were 10.8 ±2.5 and 21.4 ±3.3 µm, respectively, in haddock and 12.0 ±1.9 and 20.7 ±2.2 µm, respectively, in pollock. The values for haddock were consistent with earlier reports by Bolz and Lough (1983) and Campana (1989). In both species, increments appeared as alternate light and dark zones (Fig. 2), and the first regular increment was formed the day after hatching (Table 2). The number of increments (NI) corresponded to the chronological age in d (AGE) of the larvae (Fig. 3). The slopes of the regressions for haddock (NI=0.99 AGE, n=148, r^2=0.96, P>0.0001) and pollock (NI=1.09 AGE, n=9, r^2=0.82, P=0.0005) did not differ significantly from 1 (t-test, P=0.637 for haddock and P=0.890 for pollock).

Growth of haddock and pollock otoliths

The check at hatching was clearly visible and increments were easily distinguished in the otoliths of larvae sampled at sea (Fig. 4). The nuclear and check diameters at hatching for haddock and pollock differed in different years (ANOVA, P<0.01) (Table 3). For haddock, differences in nuclear check diameters between 1991 and 1993 were not significant (ANOVA, P>0.05). There were no significant differences among

years for yolksac check diameters for either haddock or pollock larvae (ANOVA, $P>0.05$). Within some haddock otolith nuclei, 1–3 increments were observed. Outside the nucleus, 6–8 growth increments of irregular width were observed between the nucleus check and a second well-marked check. Bolz and Lough (1983) observed 2–8 faint increments bounded by a discontinuous zone that appeared to be analogous to the yolksac check found in larval cod otoliths by Radtke and Waiwood (1980). Accordingly, I interpreted the second well-defined mark as a check resulting from yolksac resorption. The mean diameter of the yolksac check was 34.9 ±2.8 µm in haddock and 35.3 ±2.6 µm in pollock. Several (mean 7 ± 1.8) narrow (<1 µm) increments were found immediately after the yolksac resorption check. Increment width increased rapidly in subsequent increments.

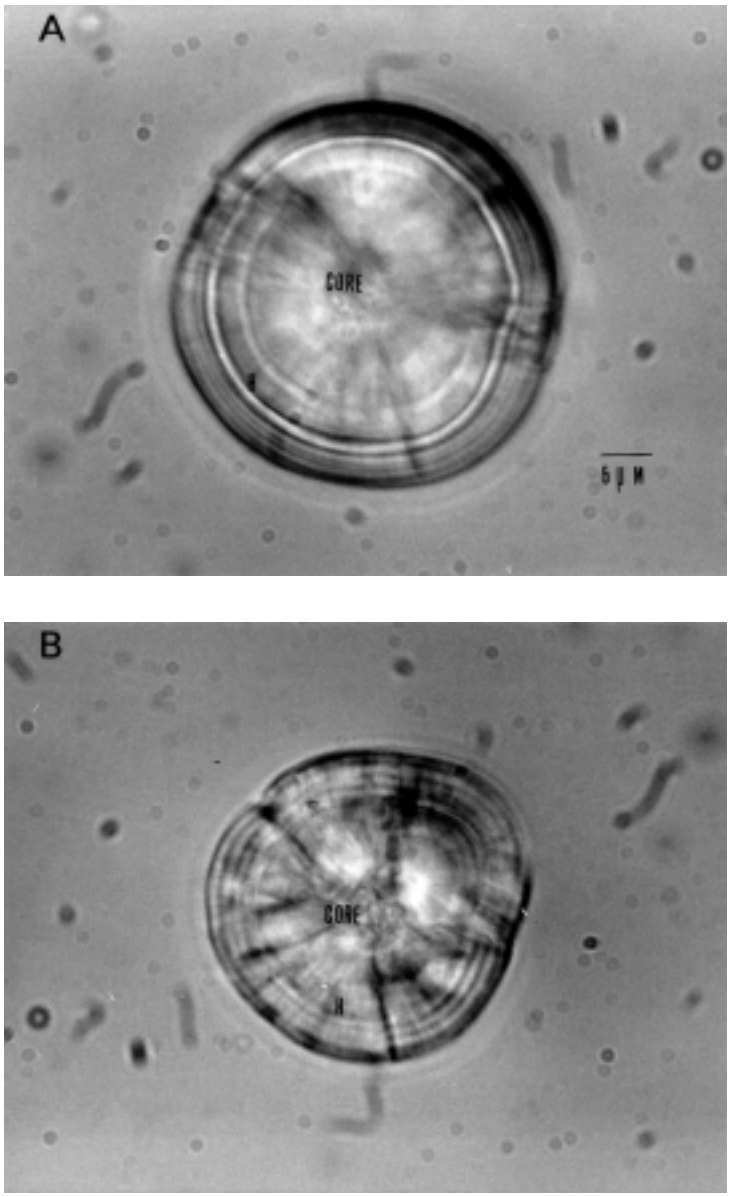

Figure 2

Light micrographs of sagittae. (**A**) Sagitta from a 5.93-mm, 5-day-old, haddock larva. (**B**) Saggita from a 4.98-mm, 3-day-old, pollock larva. H = hatch check. Growth increments appear as light and dark zones. The larvae were hatched from eggs collected from the Western and Emerald Banks area. Bar represents 5 µm.

The relation between otolith and larval fish sizes was best described by a lnln regression (Fig. 5). For haddock and pollock, significant differences were found between cruises (ANCOVA, $P<0.05$); however, no significant differences were found among years (ANCOVA, $P>0.05$) for either species (Table 4). Among haddock samples, a multiple range test revealed four homogeneous groupings in the samples from the ten cruises analyzed ($P<0.01$). The groupings were interpretable in terms of monthly sagittal growth. The first group integrated larvae from March to April; the second, larvae from May; the third, larvae from June; and the fourth, larvae from July. With pollock, the multiple range test showed three homogeneous groupings among the pollock sampled during the ten cruises ($P<0.01$). The first group integrated larvae from November to January; the second, larvae from February; and the third, larvae from March to April. It was possible to distinguish different stages in sagittal growth from otolith structure. Sagittae from the early developmental stages of haddock and pollock larvae were almost circular in shape, and there was one flat and one convex-side, accessory nucleus developed in the sagittae of postlarvae. As the larvae developed, the otoliths grew faster along the anteroposterior axis and became oval shaped.

Haddock and pollock larval and juvenile growth

For both haddock and pollock, the first otolith increment was laid down the day after hatching. Thus, the age of larvae and juveniles was indicated by the number of increments in the sagittae. Daily increments were counted in otoliths from 1121 individuals of a total of 3126 cap-

Table 2

Chronological age (from hatching), otolith diameter, and increment formation in reared larval haddock and pollock.

Chronological age (days)	Standard length (mm)	Otolith diameter (µm)	Increment	± SD	Number of larvae
Haddock					
0	4.69	26.70	0.5	0.5	18
1	4.75	27.87	1.1	0.2	15
2	5.12	30.04	2.1	0.3	21
3	5.16	32.11	3	0.4	15
4	5.68	33.03	4.1	0.4	26
5	5.74	34.03	5.1	0.3	13
6	5.86	34.04	5.8	0.6	23
7	5.90	34.41	6.6	0.8	9
8	5.86	36.45	7.3	0.4	4
9	5.77	36.92	8.5	0.5	2
10	5.84	37.58	10	—	1
11	6.19	37.67	11	—	1
Pollock					
0	4.10	24.72	1	—	1
1	3.81	26.10	1	—	1
2	4.34	29.38	2	0	3
3	5.00	28.78	3.3	0.5	3
4	4.49	32.49	4	—	1

tured. Haddock larvae and juveniles (n=602) ranged from 2.7 to 83.0 mm in SL and from 0 to 128 d in age, and pollock larvae and juveniles (n=519) from 2.8 to 23.8 mm in SL and from 0 to 84 d in age. For each year, Gompertz growth curves were fitted to describe the mean growth of larval and juvenile haddock (1991, 1992, and 1993) and pollock (1992 and 1993) (Fig. 6; Table 5). Length at hatching predicted from the curves was 4.1 mm for haddock and 4.5 mm for pollock, both within the range reported by previous studies (Fridgeirsson, 1978; Bolz and Lough, 1983; Fahay, 1983). Because the predicted inflection point for both haddock and pollock curves fell beyond the length range analyzed, the end of the first growing season had not been reached.

Although haddock larvae older than 80 d were obtained in 1991 and 1992, they were not used in the comparison of growth. Haddock growth rates (mm/d) during the first 80-d period in 1993 were different from those in 1991, and growth rates in 1993 were different from those in 1992 (ANCOVA, P<0.01) (Table 6). The 1993 cohort had the lowest growth rate. The 1991 and 1992 cohorts had similar growth rates (ANCOVA, P=0.84). The average growth rate of larvae was 0.21 mm/d during the first month and 0.42 mm/d during the second month. Growth continued exponentially from the predicted length at hatching throughout the size range of larvae and juvenile collected, there being no indication of a cessation in growth.

Table 3

ANOVA of nucleus, hatching, and yolksac checks on year for haddock and pollock larvae collected on the Scotian Shelf.

		1991	1992	1993	F	$P>F$
Haddock	Nucleus[1]	15.7	16.9	15.5	40.8	0.00
	SD	1.4	1.3	1.4		
	Hatching	22.4	25.1	23.5	34.9	0.00
	SD	2.6	3	2.1		
	Yolksac	36.6	38.7	35	0.28	0.76
	SD	3.9	4.1	2.7		
Pollock	Nucleus		14.8	15.9	38.7	0.00
	SD		1.6	1.8		
	Hatching		23.9	23.1	38.1	0.00
	SD		1.4	1.9		
	Yolksac		35.6	35.1	5.2	0.02
	SD		2.6	2.7		

[1] Nucleus check 1991 versus 1993 not significant (P>0.42).

Pollock growth rates (mm/d) varied significantly among years (ANCOVA, P<0.01) (Table 6). However,

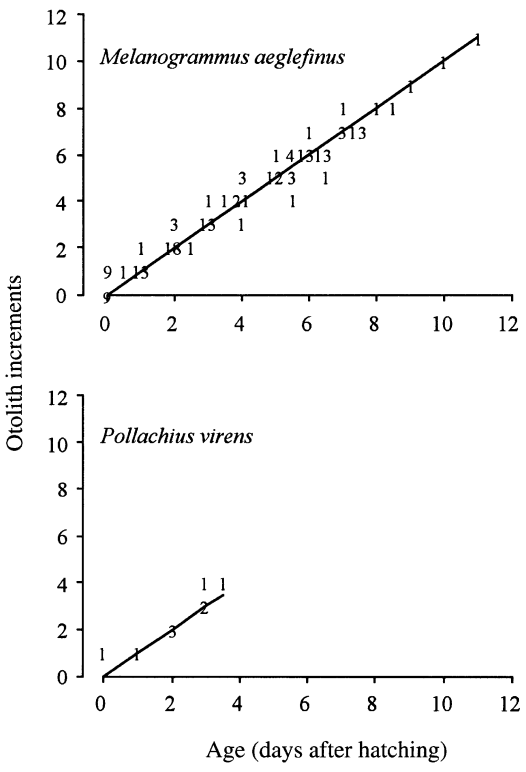

Figure 3

Number of increments enumerated on the sagittae of haddock and pollock larvae as a function of known age (days after hatching). Numbers represent the number of larvae. The number of increments (NI) corresponds to the chronological age in d (AGE) of the larvae. Haddock $NI = 0.99\ AGE$, $n = 148$, $r^2 = 0.96$, and pollock $NI = 1.09\ AGE$, $n = 9$, $r^2 = 0.82$.

the A_0 (specific growth rate at t=0) did not vary significantly (ANCOVA, P>0.05). The 1992 cohort had the higher growth rates during the first 50 d following hatching. Growth was linear at 0.18 mm/d following the predicted hatching size (1992 cohort), 0.13 mm/d (1993 cohort) through the first month, and 0.23 (1992 cohort) and 0.24 mm/d (1993 cohort) through the second month.

Discussion and conclusions

Validation of increment deposition

The present study shows that growth increments in haddock otoliths are formed daily and suggests that this is also the case in pollock. In both species, the first of the regular increments is formed on the day after hatching, and thereafter an additional increment is added each day up to 11 d for haddock and 4 d for pollock. Otoliths develop before hatching, and in haddock, 1 to 3 irregular increments are deposited prior to hatching. These types of irregular increments were not observed on larval otoliths of pollock. A few embryonic growth increments of a lamellar structure (such as I observed in haddock), have also been reported in other species (Brothers et al., 1976; Radtke and Dean, 1982; Watanabe et al., 1982; Nishimura and Yamada, 1984; Palomera et al., 1988). The spacing of embryonic increments is irregular, in contrast to regularly spaced posthatching increments, which indicates that they might not be deposited at daily intervals. Whereas Radtke and Waiwood (1980) did not observe increments formed prior to hatching in cod (*G. morhua*), they did observe regular increments that were formed daily starting one day after hatching. Brothers and McFarland (1981) noted three diffuse increments in the otolith core of French grunt (*Haemulon flavolineatum*) and speculated that they were deposited during the embryonic stage. Bolz and Lough (1983) found 1–2 poorly defined increments enclosed by the nuclear check in haddock larvae. According to the above observations, it seems reasonable to infer that the 1–3 irregular increments inside the hatch check of haddock otoliths are formed sometime during the 2–3 week egg stage (Laurence and Rogers, 1976; Fridgeirsson, 1978).

Growth of haddock and pollock otoliths

The sagittal otoliths of haddock and pollock larvae are circular in shape at the age of 35–40 d. Subsequent sagittal growth is greater along the anteroposterior plane, so that the otoliths become oval shaped in older larvae. Radtke (1989) reported that cod (*G. morhua*) sagittae change as they grow, from spherical to elongated to crenulated over a 65-d period. In haddock and pollock larvae, circular-shaped sagittae were observed until 8 mm SL, corresponding to an age of 35–40 d. Then, the sagittal shape begins to elongate as the result of growth of peripheral primordia, which corresponds to 30 mm SL (75–80 d) in haddock and 23 mm SL (80 d) in pollock. Thereafter the sagittae are not easily broken, and their shape is distinguishable from that of other gadoid species. The last changes in otolith shape correspond to the age when juveniles undergo metamorphosis to begin demersal life. Koeller et al. (1986) inferred, from a series of midwater and botton trawl surveys conducted in 1983 off southwestern Nova Scotia, that the transition to the demersal habitat by haddock occurs from June to August.

In most otoliths examined, I observed a well-defined, dark and discontinuous zone or ring laid down

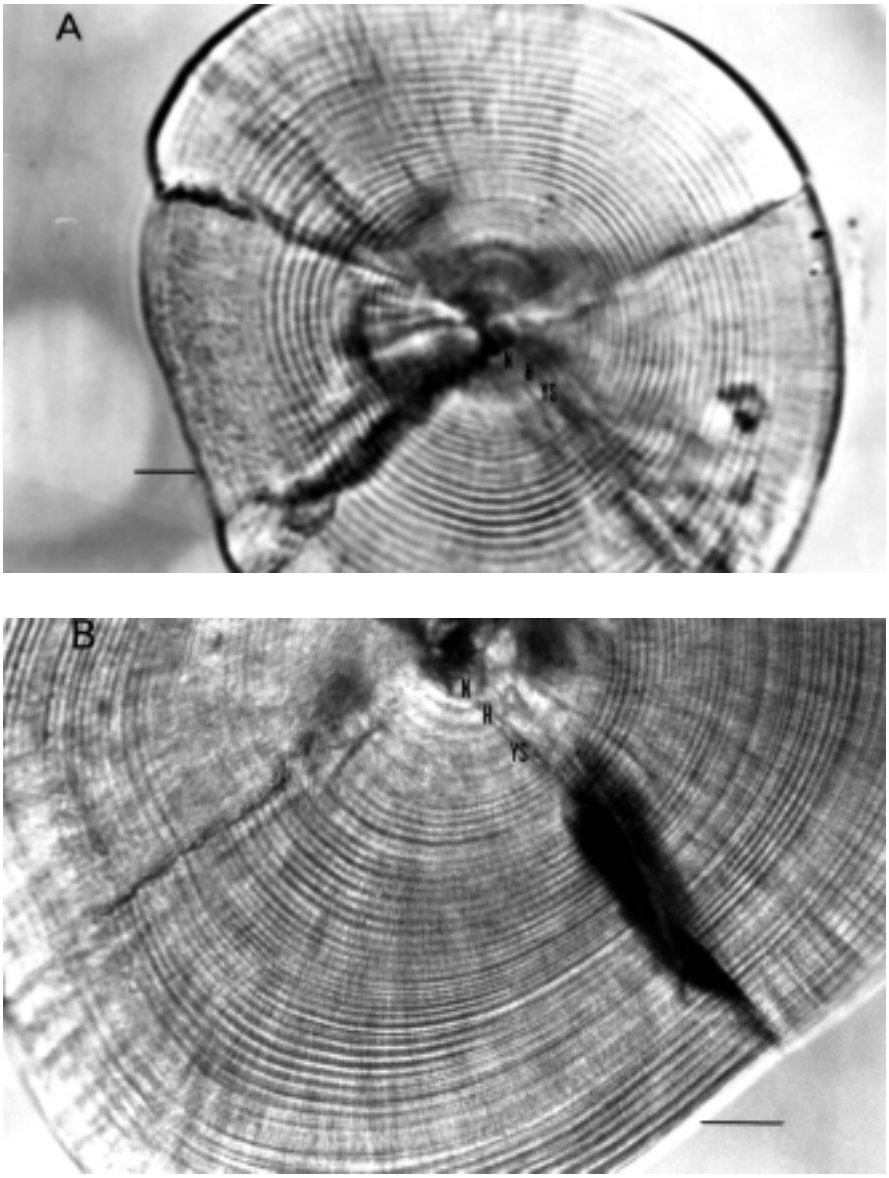

Figure 4

Light micrographs of sagittae showing different landmark checks. (**A**) Sagitta from a 13.7-mm-SL, 37-day-old haddock. (**B**) Sagitta from a 12.4-mm-SL, 50-day-old pollock. N = nuclear check, H = check at hatching, and YS = yolksac check. Bar of photograph represents 10 µm.

around the nucleus. It was the first mark presented in larval otoliths (Bolz and Lough, 1983; Radtke and Waiwood, 1980; Campana, 1989). Outside the nucleus, four to eight irregularly spaced increments were bounded by a discontinuous zone which appeared to be the yolksac check (Bolz and Lough, 1983). Laurence (1974) reported that at 7°C yolksac exhaustion occurs 6–7 d after hatching for haddock, and Fridgeirsson (1978) observed that at 7.2°C yolksac exhaustion occurs within 6 d for haddock larvae and 8 d for pollock larvae. From the regression of larval length to sagittal diameter, I estimated that yolksac resorption occurs at a standard length of 5.0 mm in haddock (at 3.5°C) and 5.1 mm in pollock larvae (at 5.0°C), corresponding to a mean age of 9 and 5 d, respectively. Fridgeirsson (1978) reported that haddock start independent feeding at 6–10 d after hatching and pollock at 8–10 d after hatching.

This suggests that the observed check is deposited at or immediately before yolksac absorption and that the number of increments between the nucleus and the absorption check reflects the duration of the yolksac phase (Fridgeirsson, 1978; Laurence, 1978; Fahay, 1983).

Haddock and pollock larval and juvenile growth

In recent years, the examination of otolith microstructure has resulted in many applications (Jones, 1992). The underlying assumption is that increments form daily. In otoliths of haddock (*M. aeglefinus*), and pollock (*P. virens*), increments are deposited daily and thus can provide accurate estimates of age (Bolz and Lough, 1983; Campana, 1989; Campana and Hurley, 1989).

The estimates of haddock growth in this study are comparable with those reported earlier. Thus, the predicted length of 4.1 mm at hatching and the average growth rate of 0.65 mm/d for 0–4 mo old larvae in the present study are similar to the values reported by Bolz and Lough (1983, 1988). The adjustment of a Laird-Gompertz model (r^2=0.99) for the entire data set correctly predicted length (Table 5). Different patterns in growth occur during ontogeny (Table 6). The average increase in length is moderate between hatching and 50 d (0.27 mm/d), high for early juveniles of 2.5–3 mo (0.68 mm/d), and moderate again (1.2 mm/d) for older juvenile. Few studies provide estimates of the age and growth of larval and juvenile pollock (Campana, 1989). The predicted length at hatching was 4.5 mm and the average growth rate of larval was 0.22 mm/d during the first 3 mo. The Laird-Gompertz model (r^2=0.98) applied to the entire set data adequately described growth. A slow increase in length occurs during the first 30 d after hatching (0.18 mm/d), and then the rate is moderate during the following 1 to 2 mo (0.23 mm/d). Finally, a stable period (0.24 mm/d) begins (Table 6). In the present study only the pelagic phase prior to metamorphosis and beginning of demersal life was examined. Nevertheless, sampling continued throughout the year and older pollock juveniles up to 80 d old (23 mm SL) were captured. The last pollock samples were collected in 1993. Juvenile pollock probably move from the oceanic zone to the shallow coastal zone after metamorphosis (Scott and Scott, 1988). Campana (1989) collected 53 pollock juveniles from the north shore of Gran Manan Island, New Brunswick, on August 1984, and the mean length of juveniles was 97.3 ± 1.9 mm. The date of capture of Campana's samples suggest that pollock juvenile move to the Scotian shore, possibly toward the Bay of Fundy, to finish their development. If pollock sharply increase their growth rate in response to improved feeding conditions during demersal lifestyle, as we observed for haddock, they could attain an average length of 106 mm by August, a size similar to that of juveniles collected by Campana. Growth rates (mm/d) varied significantly in different years, and the rates of the two cohorts showed an alternate pattern: growth was higher for the 1992 cohort during the first 45 d and higher for 1993 cohort following the first 45 d. The 1993 cohort was first detected two months later than the 1992 cohort. The adjustment of a Laird-Gompertz model (r^2=0.98) to each annual data set closely predicted length (Table 5).

Growth during the juvenile period of haddock and pollock can be divided into a series of "stanzas." The change from one stanza to the next is characterized by a discontinuity in development, such as during hatching or after a change of habitat (Ricker, 1979). Growth accelerates abruptly in fish older than 50 d in response to a shift from a pelagic to a demersal diet. Because we captured juvenile pollock immediately after the transition

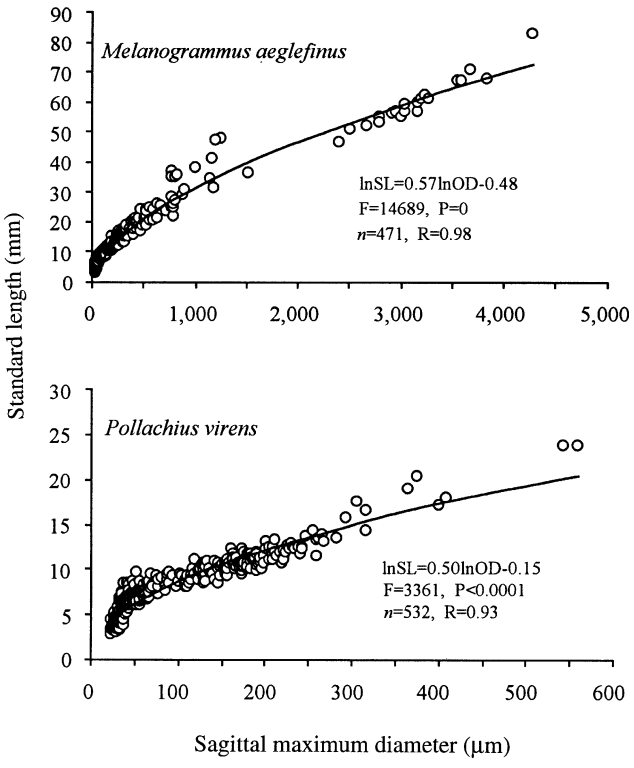

Figure 5

Standard length as a function of maximum sagittal diameter in larval pollock and haddock.

Table 4

Parameter estimates of the relationship between standard length and sagittal diameter for larval haddock and pollock collected on the Scotian Shelf. Ln$SL = a + b$LnSD. Note: The reduced correlation during March 1992 and 1993 for larval haddock is the result of differences between size of larvae and sagittal diameter at hatching.

			Intercept (a)		Slope (b)			
Species	Year	Month	Estimate	SE	Estimate	SE	n	r^2
Haddock	1991	June	0.006	0.090	0.477	0.014	37	0.97
		July	–3.140	0.442	0.898	0.055	18	0.94
	1991		–0.524	0.077	0.567	0.011	55	0.98
	1992	March	0.840	0.781	0.157	0.216	12	0.05
		April	–0.998	0.422	0.705	0.120	12	0.77
		May	0.068	0.101	0.466	0.022	65	0.87
		June	–0.002	0.167	0.500	0.027	16	0.96
		July	–0.722	0.530	0.594	0.078	5	0.95
	1992		–0.466	0.059	0.572	0.012	110	0.95
	1993	March	–4.574	0.467	1.733	0.134	134	0.56
		April	–0.618	0.162	0.612	0.038	45	0.86
		May	0.047	0.056	0.466	0.011	127	0.94
	1993		–0.469	0.032	0.564	0.007	306	0.95
		All	–0.445	0.021	0.560	0.004	471	0.97
Pollock	1991	November	2.162	0.239	–0.224	0.069	4	0.84
		December	–0.646	0.409	0.613	0.113	12	0.75
	1992	January	–0.943	0.154	0.717	0.041	91	0.77
		February	–0.095	0.093	0.482	0.019	80	0.89
		March	–1.011	0.325	0.644	0.060	17	0.88
		April	–0.463	0.469	0.568	0.087	7	0.90
	1991–1992		–0.143	0.045	0.494	0.010	211	0.92
	1993	January	–0.932	0.132	0.720	0.036	258	0.60
		February	0.694	0.119	0.326	0.024	54	0.78
		March	–0.856	0.334	0.632	0.060	5	0.97
		April	–0.392	0.505	0.538	0.091	4	0.95
	1993		–0.204	0.057	0.517	0.015	321	0.80
		All	–0.143	0.036	0.498	0.009	532	0.86

to a demersal life stage, it was possible that individuals were present in both pelagic and demersal zones at this time. Perhaps pollock juveniles were moving from the oceanic to the coastal zone; if so, this change in habitat could explain the reduction in numbers of juvenile older than 60 d in our sampling. I assume that conclusions drawn for juvenile haddock are valid only during the first eighty days for pollock. This period corresponds to the transition from a primarily pelagic to predominantly demersal life stage, which occurs when haddock reach about 20–25 mm in length (Koeller et al., 1986) and when pollock reach 10–15 mm. Although >25-mm haddock were captured in the water column, they probably had adopted a predominantly demersal life style. Thus, the acceleration in growth of >50-d juveniles could have reflected exploitation of abundant food resource after settling on the bottom (Mahon and Neilson, 1987).

In the present study, average growth rates were 0.21 mm/d in the first month and 0.42 mm/d in the second month for larval haddock and 0.18 mm/d in the first month and 0.23 mm/d in the second month for larval pollock. Growth continued exponentially

Table 5

Estimates of Gompertz model parameters for larval and juvenile haddock and pollock collected on the Scotian Shelf. L_0 = lenght at age $t = 0$, a = specific rate of growth at $t = t_0$, and k=dimensionless parameter.

Species	Year	L_0	a	k	n	r^2
Haddock	1991	2.478	0.010	4.954	114	0.99
	1992	3.609	0.006	6.172	107	0.99
	1993	4.317	0.005	5.809	381	0.99
	All	4.198	0.005	6.581	602	0.99
Pollock	1991–92	4.213	0.013	2.483	210	0.99
	1993	4.617	0.017	1.970	309	0.98
	All	4.569	0.013	2.429	519	0.98

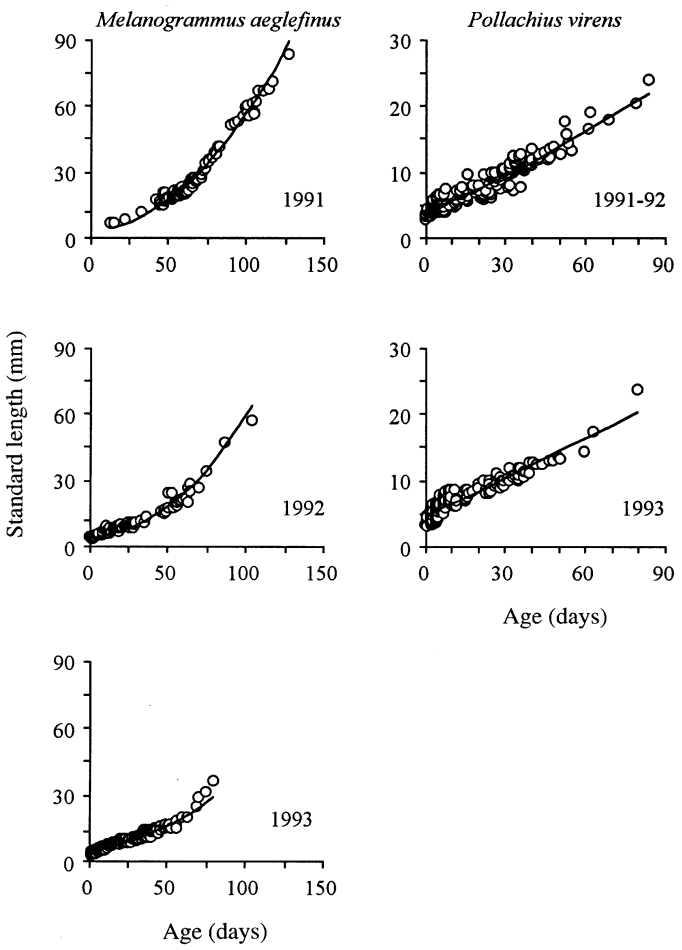

Figure 6

Estimated age versus length for larval and juvenile pollock and haddock. Lines were fitted by using the Laird-Gompertz growth model. Parameters of the model are shown in Table 5.

from the predicted length at hatching throughout the size range of larvae and juvenile collected. Otolith growth increments are suitable for estimating age, and the analysis of length–age data for young haddock and pollock on Emerald and Sable Island Banks suggests that the growth rate increases sharply at the transition from a pelagic to demersal life stage. Thus, pelagic and early demersal growth likely represents distinct "stanzas" in the growth history of these gadoids, and these "stanzas" may have different effects on recruitment variability. Rapid juvenile growth may increase juvenile survivorship by decreasing the time during which juvenile are exposed to predators (Houde, 1987). Interannual variation in juvenile growth rates may influence interannual variation in juvenile survivorship. Additional complicating factors during the pelagic phase of juvenile fish, such as different residence times and diel migrations in the water column (Koeller et al., 1986), reduce the possibility of identifing correlations between interannual variation in growth rates and environmental factors, and thereby allow predictions of recruitment success.

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Table 6

Growth rate (mm/d and %/d) of larval and juvenile haddock and pollock estimated from the Laird-Gompertz growth model.

	Haddock								Pollock					
	Growth rates (mm/d)				Growth rates (%/d)				Growth rates (mm/d)			Growth rates (%/d)		
Age (days)	1991	1992	1993	All	1991	1992	1993	All	1992	1993	All	1992	1993	All
0	0.13	0.13	0.11	0.14	4.00	3.70	2.56	3.85	0.14	0.10	0.14	3.23	1.85	3.16
5	0.16	0.16	0.12	0.16	3.86	3.59	2.56	3.72	0.15	0.10	0.16	3.02	1.85	2.96
10	0.18	0.18	0.14	0.18	3.73	3.49	2.56	3.59	0.16	0.11	0.17	2.83	1.85	2.77
15	0.21	0.21	0.16	0.21	3.60	3.38	2.56	3.47	0.17	0.13	0.18	2.66	1.84	2.60
20	0.24	0.24	0.18	0.24	3.48	3.28	2.55	3.35	0.19	0.14	0.19	2.49	1.84	2.43
25	0.28	0.27	0.21	0.27	3.36	3.19	2.55	3.23	0.20	0.15	0.20	2.33	1.84	2.28
30	0.32	0.31	0.24	0.31	3.24	3.09	2.55	3.12	0.21	0.16	0.21	2.19	1.84	2.14
35	0.36	0.35	0.27	0.35	3.13	3.00	2.55	3.01	0.21	0.18	0.22	2.05	1.84	2.00
40	0.40	0.39	0.31	0.39	3.02	2.91	2.55	2.91	0.22	0.20	0.23	1.92	1.83	1.88
45	0.45	0.44	0.35	0.44	2.92	2.83	2.55	2.81	0.23	0.22	0.24	1.80	1.83	1.76
50	0.50	0.49	0.40	0.48	2.82	2.74	2.55	2.71	0.23	0.24	0.24	1.69	1.83	1.65
55	0.56	0.54	0.45	0.53	2.72	2.66	2.55	2.62	0.24	0.26	0.24	1.58	1.83	1.54
60	0.62	0.60	0.52	0.59	2.63	2.58	2.55	2.53	0.24	0.28	0.25	1.48	1.82	1.45
65	0.68	0.66	0.59	0.64	2.54	2.51	2.55	2.44	0.24	0.31	0.25	1.39	1.82	1.36
70	0.74	0.73	0.67	0.70	2.45	2.43	2.55	2.36	0.24	0.34	0.25	1.30	1.82	1.27
75	0.81	0.80	0.76	0.76	2.37	2.36	2.55	2.28	0.24	0.37	0.25	1.22	1.82	1.19
80	0.88	0.87	0.86	0.82	2.29	2.29	2.55	2.20	0.24	0.41	0.25	1.14	1.82	1.12
85	0.95	0.94		0.88	2.21	2.22	2.12	0.24		0.24		1.07		1.05
90	1.02	1.02		0.94	2.13	2.16	2.05							
95	1.09	1.10		1.01	2.06	2.09	1.98							
100	1.17	1.19		1.07	1.99	2.03	1.91							
105	1.24	1.27		1.14	1.92	1.97	1.85							
110	1.32			1.20	1.85		1.78							
115	1.39			1.27	1.79		1.72							
120	1.47			1.33	1.73		1.66							
125	1.54			1.40	1.67		1.61							
130	1.62			1.46	1.61		1.55							

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