Otolith microstructure of three larval gadids in the Gulf of Maine, with inferences on early life history

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A detailed analysis of the assumptions underlying the application of otolith microstructure was undertaken for three gadid species from the Gulf of Maine. Daily increment counts provided a precise and accurate index of age in cod (*Gadus morhua*) and appeared to do so in haddock (*Melanogrammus aeglefinus*). However, the widths of increments formed shortly after hatch in cod and haddock otoliths approached the resolution limit of light microscopy, resulting in an underestimation of age by 2–3 d for all fish. Daily increments were also formed in the otoliths of pollock (*Pollachius virens*) but, perhaps because of more severe resolution problems, the microstructure associated with the early larval stage was unclear. Factors that could confound growth back-calculation efforts included differing otolith length – larval length relationships among samples and an inverse correlation between hatch check diameter and temperature. Estimates of hatch date and growth rate developed in this study were not affected by slight deviations from the underlying assumptions, but might be affected by such deviations under different environmental conditions. Larval pollock growth was comparable to that of cod and haddock, despite a later hatch date. Pollock hatched primarily in November, while peak dates for cod and haddock hatching occurred in March–April and May, respectively. Cod on Georges Bank hatched significantly earlier than those on Browns Bank, although the latter included a less abundant component that hatched in the fall.

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L'examen des otolithes de trois espèces de gadidés du Golfe du Maine a permis de faire une analyse détaillée des hypothèses sous-jacentes à l'utilisation de la microstructure des otolithes. L'évaluation de la croissance journalière des otolithes a fourni un indice précis de l'âge chez des Morues franches (*Gadus morhua*) et apparemment aussi chez des Aiglefins (*Melanogrammus aeglefinus*). Cependant, la largeur des anneaux de croissance formés peu après l'éclosion sur les otolithes des morues et des aiglefins est très près de la limite de résolution d'un microscope photonique, et cela a entraîné ici des sous-estimations de l'âge, de l'ordre de 2–3 jours, chez tous les poissons. Des anneaux journaliers de croissance se forment aussi sur les otolithes de la Goberge (*Pollachius virens*), mais, sans doute à cause de problèmes de résolution plus graves, la microstructure associée aux premiers stades larvaires n'était pas claire. Parmi les facteurs qui peuvent fausser le rétrocalcul de la croissance, il faut mentionner les variations appréciables du rapport longueur des otolithes : longueur de la larve entre les échantillons et la corrélation inverse entre le diamètre des marques d'éclosion et la température. Les estimations relatives à la date d'éclosion et au taux de croissance obtenues au cours de cette étude n'étaient pas affectées par les faibles écarts par rapport aux hypothèses de départ, mais il n'est pas exclus que ces écarts puissent avoir une influence plus forte en présence de conditions différentes du milieu. La croissance larvaire de la Goberge était comparable à celle de la Morue franche ou de l'Aiglefin, même si la date d'éclosion était plus tardive. Chez la Goberge, l'éclosion avait lieu surtout en novembre, alors qu'elle avait lieu surtout en mars–avril chez la Morue et en mai chez l'Aiglefin. L'éclosion était significativement plus hâtive chez les morues du banc Georges que chez les morues du banc Browns, bien qu'une petite portion des morues du banc Browns aient éclos à l'automne.

[Traduit par la revue]

Introduction

The utility of otolith microstructure examination to determine age and back-calculate growth is based upon two principles: firstly, that otolith growth occurs incrementally on a daily basis, and secondly, that there is a correspondence, on average, between fish growth and otolith growth (Pannella 1971; Brothers et al. 1976; review by Campana and Neilson 1985). The formation of daily growth increments is now considered ubiquitous, and provides the means for the precise determination of age and date of hatch. The correspondence between fish and otolith growth theoretically allows growth (size at age) to be backcalculated. However, the assumptions upon which these principles are based are seldom tested. While the daily periodicity of increment formation can often be safely assumed, substantial errors in interpretation are possible (Campana and Neilson 1985). The resolution limits of light microscopy may also introduce serious error into the interpretation of slow-growing otoliths, particularly those of temperate, pelagic larvae (Geffen 1982; Campana et al. 1987; Jones and Brothers 1987). Finally, apparent correlations between fish and otolith growth may not persist at the daily level, thus confounding attempts at backcalculation (Brothers 1981; Gutiérrez and Morales-Nin 1986; Bradford and Geen 1987).

The objective of this paper is to assess the utility of examining otolith microstructure in the study of the early life history of three gadid species in the Gulf of Maine. General characteristics of the otolith microstructure of larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) have been used in the preparation of specific (Bolz and Lough 1983) and generalized (Campana and Hurley 1989) growth models. The intent here is to more fully examine the assumptions upon which these studies were based and provide new early life history information for populations on Browns and Georges banks. Since little is known of larval pollock (*Pollachius virens*), preliminary results concerning the otolith microstructure and larval growth of this species will also be presented. Finally, this paper will examine variation in some critical otolith characteristics in relation to spatial and temporal variations in the environment.

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Materials and methods

Cod, haddock, and pollock larvae were collected during seven cruises over a fixed survey grid as part of the Southwest Nova Scotia Fisheries Ecology Program ichthyoplankton survey. The surveys encompassed 97 stations to the south, east, and west of Nova Scotia, including portions of Georges Bank (Fig. 1). Cruises were conducted in March and April of 1984 and monthly between February and June of 1985, although weather restricted grid coverage in some months (Table 1). Each station was sampled with paired bongo nets fitted with 61-cm frames, 333-μm Nitex mesh, and mouth-mounted flowmeters. Tows were made obliquely to within 5 m of the bottom (to a maximum of 200 m) and immediately replicated. Water temperature was recorded at each station with a conductivity, temperature, and depth recorder. Full sampling details and cruise-by-cruise station locations are documented elsewhere (P. Hurley and S. E. Campana, unpublished data).

Unsorted samples were preserved in 5% formalin−saltwater adjusted to a pH of 8.0−9.0 with sodium carbonate; the latter retarded acidic degradation of the otoliths. Samples were transferred to 95% ethanol within 3 weeks of collection, and stored therein for up to 6 months. Before removal of otoliths, total length of larvae was measured to the nearest 0.1 mm. Both pairs of sagittal and lapillar otoliths were removed, cleansed of adhering tissue, and mounted individually on microscope slides with Krazy Glue (Campana and Neilson 1985). Otoliths with diameters exceeding 40 μm were polished with lapping film (3-μm grit) before microstructural examination. Otoliths showing evidence of formalin degradation (brown discolouration, pitting) were not considered further. Degraded otoliths constituted approximately 20% of the total number (primarily from cruise H135), although the degraded proportion within a sample varied substantially among samples. Microstructural examinations were made with a research-quality compound microscope at 1250×; the functional resolution limit of this microscope was previously estimated to be 0.25 μm (Campana et al. 1987). Measurements of otolith and hatch check diameter were made with an ocular micrometer to the nearest micrometre, with the difference between the two measurements hereafter defined as the growth diameter. Criteria for definition of the hatch check were those of Bolz and Lough (1983), Bergstad (1984), and Dale (1984). All daily increment counts were replicated by the same reader. Unless stated otherwise, the mean measurement and count values for each otolith type within a larva were used in all analyses.

Indices of potential loss of resolution during increment counts were generated through the increment width estimation procedure described in Campana et al. (1987). Briefly, this involved fitting a logistic curve to the increment count associated with each otolith growth diameter (OGD = otolith diameter minus hatch diameter), and then using the fitted model to estimate increment width in the first few days after hatch. Specifically, the otolith growth diameter (OGD) was related to increment count (C) in the following logistic equation:

$$\mathrm{OGD} = a + b(1 + \exp(-c(C-d)))^{-1}$$

where a, b, c, and d are model parameters. Increment width on day i was then calculated as $(\mathrm{OGD}_i - \mathrm{OGD}_{i-1})/2$ for each of the samples.

A single sample of 53 pollock juveniles was collected with a beach seine from the north shore of Grand Manan Island, New Brunswick, on August 15, 1984. The mean length of the fish was 97.3 mm (SE = 1.9). The sample was frozen upon collection and thawed at the time of otolith removal. Otoliths were treated as described above.

To confirm the frequency of increment formation in larval pollock otoliths, a small validation experiment was conducted between February 20 and March 15, 1984. Pollock were reared from the egg stage to an age of 24 d under a diel light cycle (12 h light : 12 h dark) and temperatures of about 6°C. Larvae were fed twice daily with *Artemia* and (or) rotifers. Sampled larvae (N = 13) were preserved in 95% ethanol before otolith removal; microstructural examinations were made as described above without knowledge of larval age or sampling frequency.

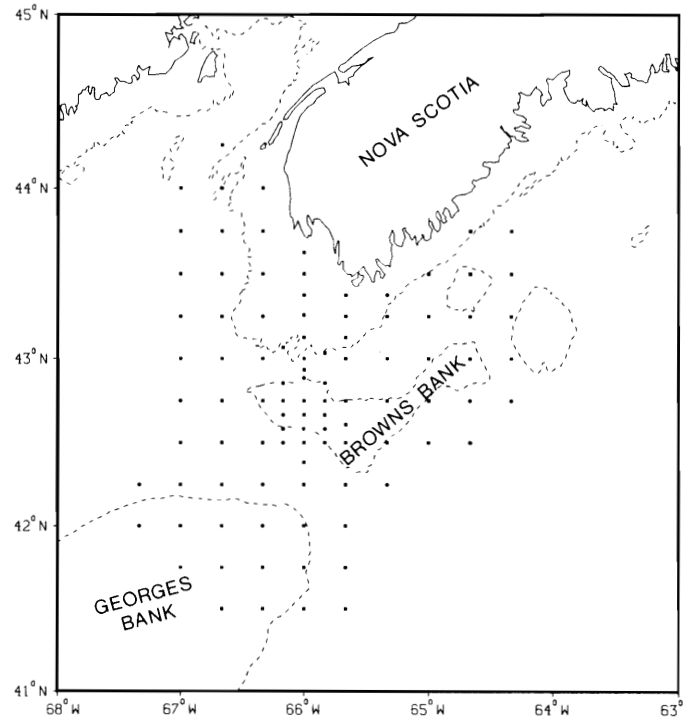


FIG. 1. The location of sampling stations relevant to this study during the ichthyoplankton survey of southwest Nova Scotia in 1984 and 1985. The 100-m depth contour is indicated by broken lines.

Hatch dates were back-calculated for each of the species through subtraction of larval age from the date of collection. Pooled within-year samples were then used to assess the frequency distribution of hatch dates. In the case of pollock, hatch date distribution was determined from a sample of juveniles rather than the smaller number of larvae that was available. Since increments in the inner region of the juvenile pollock lapilli were often difficult to resolve, unresolved increment number in all 53 juveniles was interpolated using an empirical relationship (age = exp(6.39−(1/(−0.425 + (0.195(ln Lapd))))) + 30) between the diameter of the unresolved region (Lapd) and increment number at equivalent diameters in fully resolved lapilli (N = 32). The maximum deviation between predicted and observed increment counts in fully resolved juvenile lapilli was 5 (N = 15). The mean number of interpolated increments in the partially resolved lapilli was 50. While the interpolation procedure appears to provide a reasonable approximation of unresolved increment number, the relative imprecision of the pollock hatch dates should be kept in mind during their interpretation.

Parameters for larval and otolith growth models were estimated for two regions, Browns Bank − Southwest Nova Scotia and Georges Bank, based upon presumed stock boundaries (Bowen 1987) and hydrographic regimes (Smith 1983; Perry and Hurley 1986). Daily temperature values were those employed by Campana and Hurley (1989) for the appropriate date and region. All linear and nonlinear regression parameters were estimated by least-squares methods. Residuals from the models were given careful examination, particularly near the origin. Models were accepted only in the absence of patterns in the residuals. The significance level was 0.05 for all tests.

Results

Factors influencing otolith size

At the time of hatch, lapillus diameter exceeded that of sagittae in all three gadid species. Subsequent lapillar growth in cod and haddock was proportional to that of the larva, with the caveat that the residuals from the regression of larval length

TABLE 1. Summary of cruises represented in this study

	Cruise	Date	Total no. of stations sampled	No. of larvae examined	
				Cod	Haddock
1984	H114	March 12–30	54	7	67
	H116	April 16–27	59	100	0
1985	H130	February 4–22	93	17	0
	H132	March 11–29	49	62	13
	H133	April 2–17	90	236	53
	H135	May 6–16	57	201	435
	H137	June 3–14	59	49	974

on lapillar diameter exhibited a slight but persistent positive anomaly between 50 and 90 μm. The anomaly may have been a measurement artifact associated with the allometric growth of the lapillus; at a diameter of approximately 40–50 μm, the axis of maximum diameter shifted orthogonally, necessitating a shift in the measurement axis. The pollock data were too few to allow for a similar examination. However, the form of the pollock lapillus–larva relationship differed in that it was semi-logarithmic (Table 2; Fig. 2).

The lapillus–larva relationship for cod and haddock differed significantly among regions, years, and cruises, although the contribution of these factors was difficult to assess (ANCOVA, $p < 0.01$) (Table 2). Among haddock samples, one of the four cruise collections differed significantly (June 1985), while among cod, multiple range analyses showed five homogeneous groupings among the eight cruise collections ($p < 0.05$). The groupings and factor means were not readily interpretable in terms of month or region. However, all of these results should be interpreted cautiously, because of the residual anomalies noted above.

Sagittal growth proceeded more rapidly than lapillar growth in all three species, despite smaller initial size. All of the sagitta–larva relationships were best described by a ln–ln regression (Fig. 3). For cod, no significant differences were found among cruises, regions, or years (ANCOVA, $p > 0.1$) (Table 2). Models assuming a common slope and different intercepts and those with different slopes and intercepts for each cruise were equally plausible for haddock, and could not be differentiated on the basis of explained variance. However, both models were similar in documenting significant differences among cruises (ANCOVA, $p < 0.05$) (Table 2). Multiple range tests differed depending on the choice of model. No such tests were possible with the pollock data. However, the non-random distribution of the pollock residuals suggested that the relationship may not be linear (Fig. 3).

The diameter of each otolith at the time of hatch was determined through measurement of its hatch check diameter. Not surprisingly, hatch check diameter significantly influenced otolith diameter when the latter was small ($p < 0.05$); the relationship was nonsignificant in otoliths greater than 30 μm in diameter. Hatch check diameters of the left and right lapilli were significantly correlated with each other in both cod and haddock, as were those of the sagittae ($p < 0.01$). Mean lapillar and sagittal hatch check diameters were also significantly correlated among themselves ($p < 0.05$), indicating a high degree of intralarval correspondence.

There were no significant differences in hatch check diameter for cod or haddock among cruises or between Browns and Georges Bank (Scheffé's test, $p > 0.05$). However, there was an inverse relationship between hatch check diameter and temperature at the time of hatch in both the sagittae and lapilli (Table 3, Fig. 4).

Otolith microstructure

The microstructural features of the cod otoliths were similar to those of haddock and have largely been described elsewhere (Radtke and Waiwood 1980; Gjøsaeter and Tilseth 1982; Bolz and Lough 1983; Bergstad 1984; Dale 1984; Campana and Hurley 1989). Two features not discussed elsewhere influenced microstructural interpretation. The hatch check in cod was sharply demarcated, while that of haddock appeared to consist of two equally prominent, adjacent checks. The interspecific distinction could often be used to distinguish between the species. It also introduced a small degree of error (± 1–2) into the increment counts of haddock otoliths, since the true hatch check could not be determined. As a matter of convention, the inner of the two checks was assumed to represent the time of hatch. A second, more influential feature was the presence of prominent subdaily increments in a zone of rapidly increasing increment width in the lapilli (and, to a lesser extent, in the sagittae) of cod and haddock. This zone occurred between the ages of 20 and 40 d (corresponding to a diameter of 40–60 μm) and, in some cases, made the differentiation of daily and subdaily increments extremely difficult. Continuity in increment width was often the only effective criterion in this region, particularly if the region was even slightly over-polished. Interpretation of the remainder of the otolith was largely unambiguous. Despite the presence of this potentially confusing (but narrow) zone, lapilli were generally easier to interpret than were sagittae because of their more clearly defined increments, the ease of their preparation, and the absence of accessory primordia.

The visual contrast of the pollock otolith microstructure was exceptionally poor. Otoliths with a diameter of less than approximately 40 μm often appeared uniform across the otolith surface (at least initially), although increments were clearly expressed in regions of greater diameter (Fig. 5). Visual uniformity was characteristic of samples from 1984 and 1985, from a variety of locations and sampling dates; it was uncharacteristic of dozens of sympatric species collected from similar habitats (unpublished data). Increment counts of a small sample of known-age, laboratory-reared pollock larvae were consistent with the true age of the larvae (Table 4), but the degree of uncertainty exceeded that associated with other species (unpublished data). Increments in laboratory-reared sagittae and lapilli were more difficult to see than those of the field samples, in keeping with previous studies (Campana and Neilson 1985).

TABLE 2. Parameter estimates for the regression model $L = a + b(\mathrm{OD})$ relating larval length (L) to otolith diameter (OD) for larval cod, haddock, and pollock

	Otolith type	Model type	Region	Year	Month	Intercept (a) Estimate	Intercept (a) SE	Slope (b) Estimate	Slope (b) SE	N	R^2
Cod	Lapillus	1	Browns, Georges	1984	Mar., Apr.	0.055	0.093	0.106	0.002	116	0.98
			Browns	1985	Feb.	1.308	0.399	0.090	0.005	15	0.96
					Mar.	−1.241	0.273	0.152	0.008	39	0.91
					Apr.	−0.024	0.061	0.113	0.002	181	0.98
					May	0.129	0.147	0.115	0.002	72	0.97
					June	0.420	0.561	0.114	0.008	24	0.91
			Georges	1985	Apr.	−1.180	0.599	0.141	0.018	14	0.83
					May	2.044	1.754	0.104	0.010	26	0.82
			All*	All	All	0.183	0.055	0.109	0.001	523	0.97
	Sagitta	3	All	All	All	−0.620	0.023	0.600	0.006	507	0.95
Haddock	Lapillus	1	Browns	1985	Apr.	0.852	0.540	0.078	0.015	35	0.45
					May	0.243	0.336	0.091	0.010	118	0.43
					June	−0.681	0.129	0.124	0.003	388	0.83
			Georges	1984	Mar.	−0.118	0.413	0.098	0.011	67	0.56
			All*	All	All	−0.790	0.097	0.125	0.002	614	0.83
	Sagitta	3	Browns	1985	Apr.	−0.608	0.453	0.558	0.135	36	0.33
					May	−0.677	0.201	0.570	0.061	118	0.43
					June	−1.015	0.052	0.690	0.014	388	0.86
			Georges	1984	Mar.	−1.566	0.329	0.826	0.096	69	0.52
			All*	All	All	−1.135	0.046	0.718	0.013	614	0.84
Pollock	Lapillus	2	Browns	1984, 1985	All	−24.633	0.870	8.166	0.213	46	0.97
	Sagitta	3	Browns	1984, 1985	All	−0.706	0.073	0.609	0.017	45	0.97

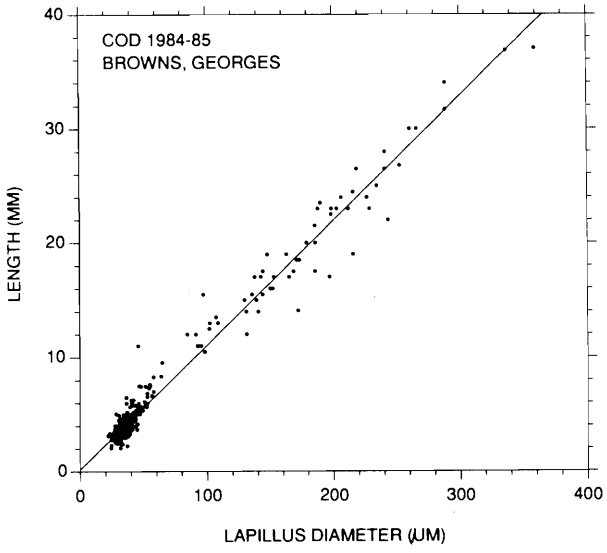
NOTE: Models have been ln-transformed to stabilize the variance where appropriate (model types 1, 2, and 3 are untransformed, ln OD, and ln L − ln OD, respectively). Where significance levels allowed, data have been aggregated across cruises.
*Aggregated values in the presence of among-group differences.

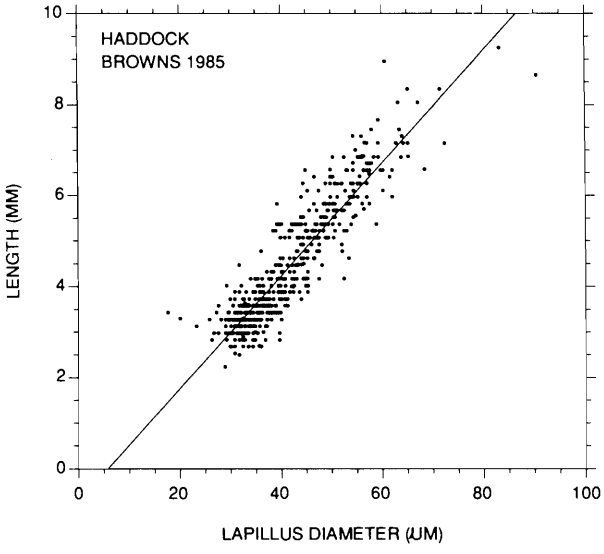
TABLE 3. Regression models for larval cod and haddock collected in 1985 relating lapillar and sagittal hatch check diameters to temperature on the date of hatch

	Intercept (a) Estimate	Intercept (a) SE	Slope (b) Estimate	Slope (b) SE	N	p	R^2
Cod							
Browns Bank							
Lapillus	23.53	0.32	−0.2732	0.0767	312	0.0004	0.04
Sagitta	17.96	0.30	−0.2120	0.0723	297	0.0004	0.03
Georges Bank							
Lapillus	27.82	5.24	−1.128	1.212	42	0.36	0.02
Sagitta	27.73	6.22	−2.376	1.424	33	0.10	0.08
Haddock							
Browns Bank							
Lapillus	22.97	0.59	−0.2158	0.1009	433	0.03	0.01
Sagitta	18.00	0.51	−0.1513	0.0871	436	0.08	0.01

NOTE: The model was $H = a + bT$, where H is hatch check diameter (μm) and T is temperature (°C).

The resolution limits of light microscopy introduced a small but significant bias into the increment counts of all three gadid species; increments too narrow to resolve as individual units underrepresent true increment number when counted. While increment width increased curvilinearly with distance from the nucleus, increments in the immediate vicinity of the nucleus were only slightly broader than the functional resolution limit of the microscope (0.25 μm). Resolution limitations were indicated by the fact that a greater number of growth increments were visible in the larger of the two sagittae within each larva. In all large samples of larvae, intersagittal differences in growth radius were significantly correlated ($p < 0.01$) with the corresponding differences in increment number, suggesting resolution-limited visibility of the increments in the smaller otolith. A similar relationship was observed among the lapilli. The statistical significance of this relationship decreased as the age range in the data increased. Further support for the presence of resolution effects was suggested by intralarval comparisons of increment counts between otolith types; intralarval increment counts were highly correlated both within an otolith type and between lapilli and sagittae (slope = 1.0 ± 0.05; $R^2 > 0.95$) in both cod and haddock (Fig. 6). However, the intercept term for the regression of sagittal counts on lapillar counts was highly significant ($p < 0.001$), and indicated that





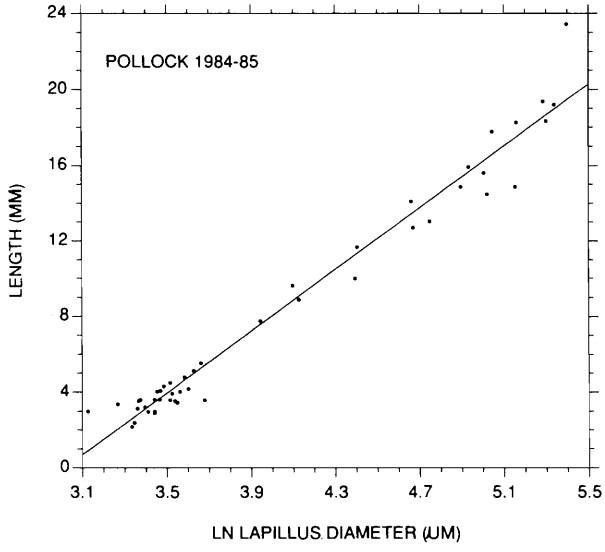
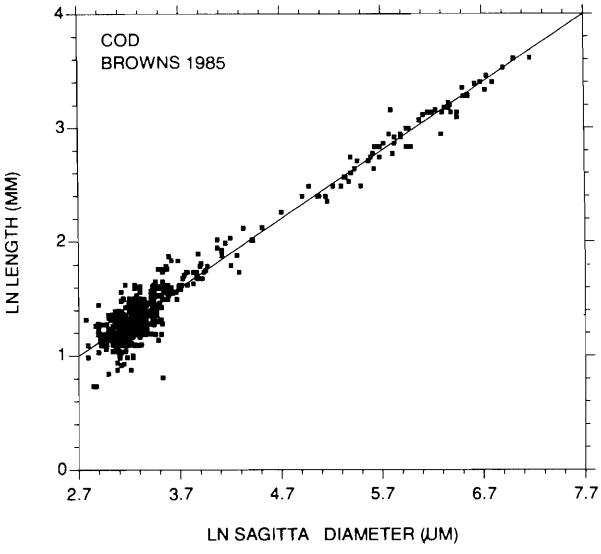
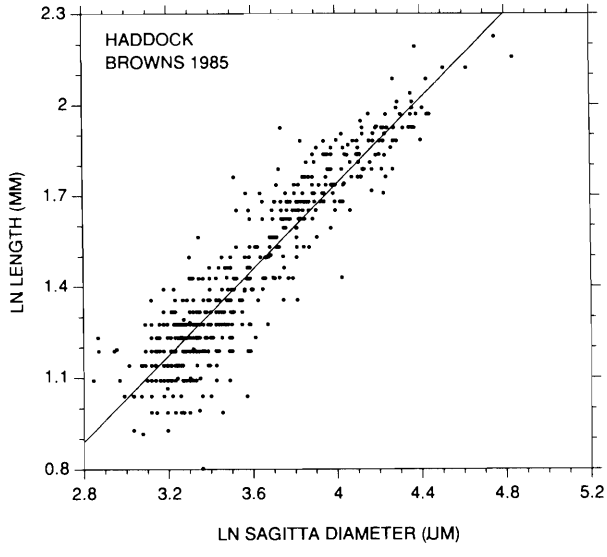


FIG. 2. Total length as a function of maximum lapillus diameter in larval cod, haddock, and pollock. Data have been pooled for demonstration purposes, despite the presence of significant differences among collections of cod and haddock (Table 2).





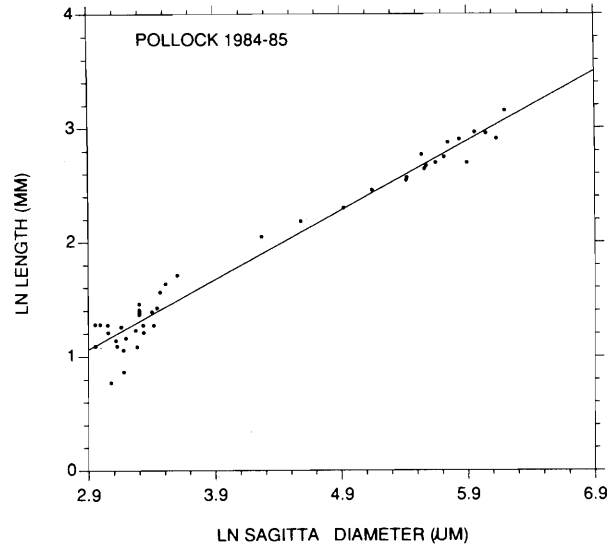


FIG. 3. Total length as a function of maximum sagitta diameter in larval cod, haddock, and pollock. Data have been pooled for demonstration purposes, despite the presence of significant differences among collections of haddock (Table 2).

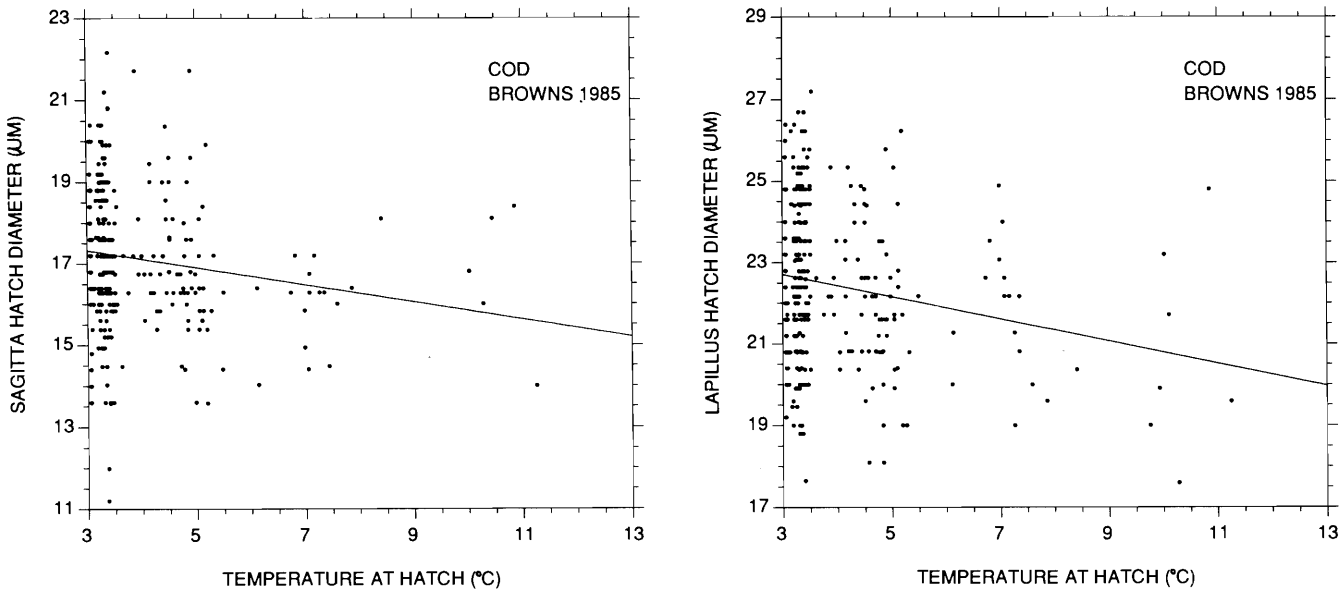


FIG. 4. The relationship between hatch check diameter and temperature on the date of hatch for lapilli and sagittae in larval cod collected in 1985 in and around Browns Bank. Both regressions are statistically significant.

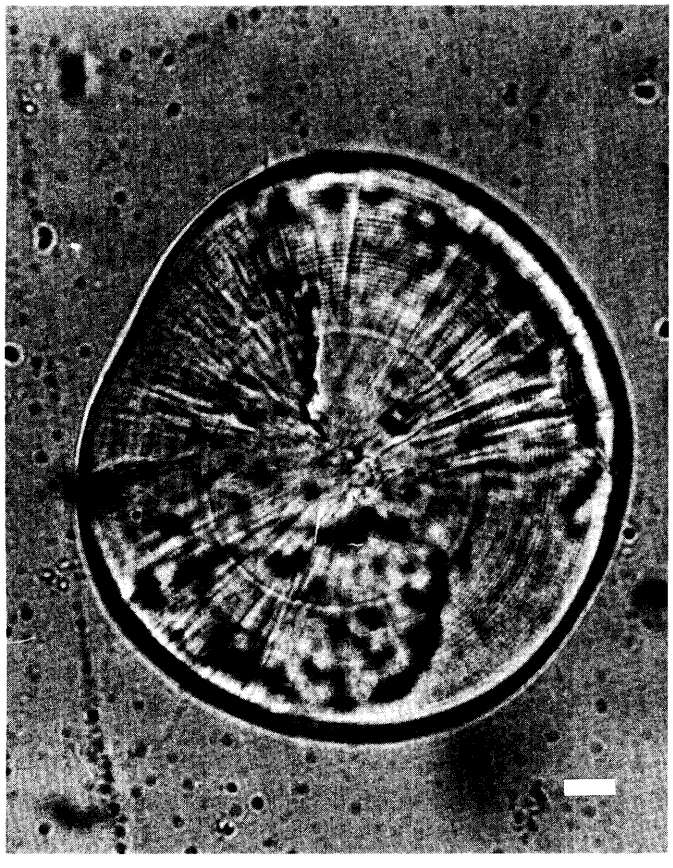


FIG. 5. Light micrograph of the otolith microstructure of a typical larval pollock sagitta. Larval length was 8.9 mm. Note the weak or absent expression of growth increments medial to the check (indicated by arrow). The check has a diameter of 46 μm, which indicates that it was formed well after the time of hatch. Scale bar = 10 μm.

the latter exceeded the former by an average of 2.6 and 1.6 for cod and haddock, respectively. The most likely source of this interotolith discrepancy was reduced resolution of the increments encircling the nucleus in the smaller sagitta. Similar resolution effects were suspected in the pollock otoliths on the basis of the very narrow increments present.

TABLE 4. Preliminary results of experiment testing the frequency of increment formation in laboratory-reared larval pollock

Sample	*N*	Age (d)	Mean increment count
1	3	1	0.9
2	6	9	7.0
3	4	17	14.5

NOTE: Microstructural interpretations were made without prior knowledge of the experimental conditions, including duration of experiment and sampling frequency.

The magnitude of the count bias associated with unresolved growth increments appeared to be small. Increment widths at age 1 d in both sagittae and lapilli were close to the resolution limit of the microscope system (0.25 μm) in cod and haddock from all cruises (Fig. 7). Increment widths of laboratory-reared cod at age 1 d (Campana and Hurley 1989) were similar to or less than those of the field-collected larvae, and were associated with a 1 to 2-d age underestimation in the lapilli (4−5 d in the sagittae). Therefore, similar or smaller errors were assumed to have been incorporated into the ages of the field-collected larvae. In addition, the increment widths increased rapidly with age, suggesting that unresolved increments were associated only with the very youngest larvae. Accordingly, daily increment counts (plus one, corresponding to the age at hatch check formation; Bergstad 1984; Dale 1984) were taken to accurately represent the true age of cod. Since haddock increment widths at age 1 d tended to be larger than those of cod, a similar conclusion was reached for haddock.

Early life history

When an exponential growth model was fit to larval pollock data aggregated from 1984 and 1985 samples, the fitted growth rate was comparable to that of larval cod and haddock exposed to an ambient temperature of 5°C (Campana and Hurley 1989) (Fig. 8). There were too few data to test for year effects or to fit an age- and temperature-mediated growth model.

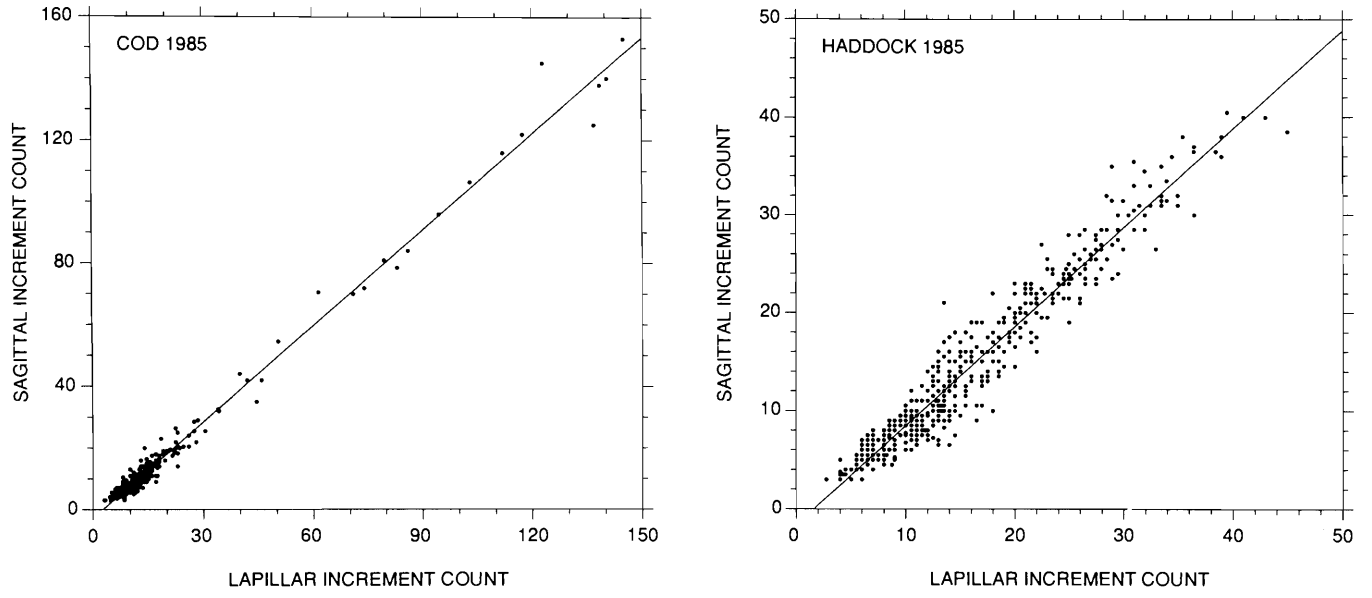


FIG. 6. Precision of daily increment counts in larval cod and haddock as indexed by intralarval comparisons of counts between lapilli and sagittae. Both regression slopes are not significantly different from 1.0.

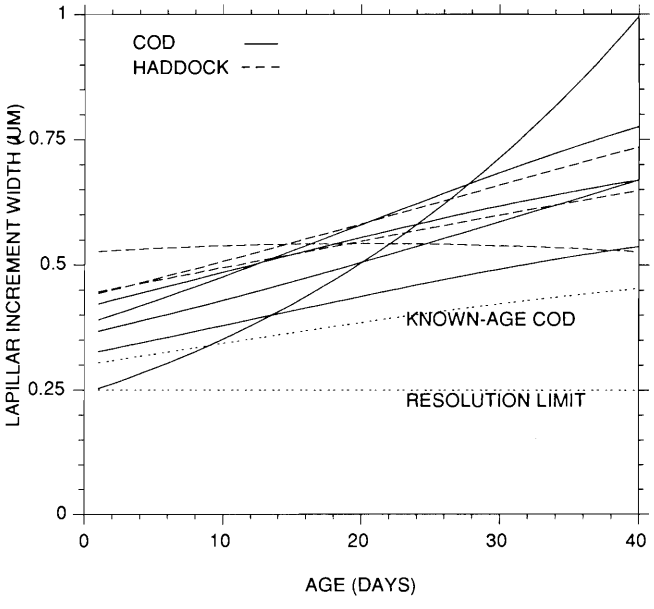


FIG. 7. Estimated widths of daily increments in larval cod and haddock lapilli collected off southwest Nova Scotia in 1985. Each curve represents the increment width − age relationship for a single cruise collection (cod: cruises H114, H132, H133, H135, and H137; haddock: cruises H114, H133, H135, and H137). The sample of known-age cod was reared in the laboratory (Campana and Hurley 1989). the theoretical resolution limit of the light microscope (indicated) was 0.25 μm.

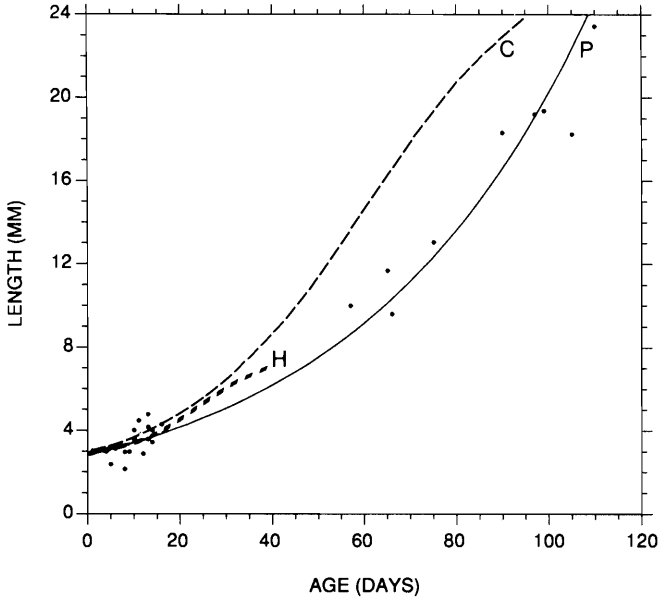


FIG. 8. Exponential growth model fitted to larval pollock (P) data collected in 1984 and 1985. Predicted growth curves for larval cod (C) and haddock (H) at 5°C were generated using an age- and temperature-mediated growth model developed elsewhere (Campana and Hurley 1989). The selection of the 5°C temperature value was arbitrary.

Hatch date distributions differed among the three species (Fig. 9). Peak hatch dates for cod occurred in mid-March to early April, although some were hatched in the late fall. Hatching continued until at least June. While spawning by cod on Browns Bank was more protracted than that of cod on Georges Bank, median hatch dates on Brown Bank were significantly later than those on Georges Bank (Mann–Whitney, $p < 0.01$). Haddock hatching on Browns Bank began in March, but hatch dates were more sharply defined than those of cod, and were centred in May. The pollock hatch dates occurred much later, with a peak in mid-November. Although the cod and haddock hatch date distributions appear to be multimodal, the irregular frequency distributions are at least partially a function of sampling date, with each cruise collection contributing a mode of young, numerically abundant larvae. The normal distribution of pollock hatch dates supports this concept.

Discussion

The primary assumption upon which otolith microstructure examination is based is the daily frequency of increment

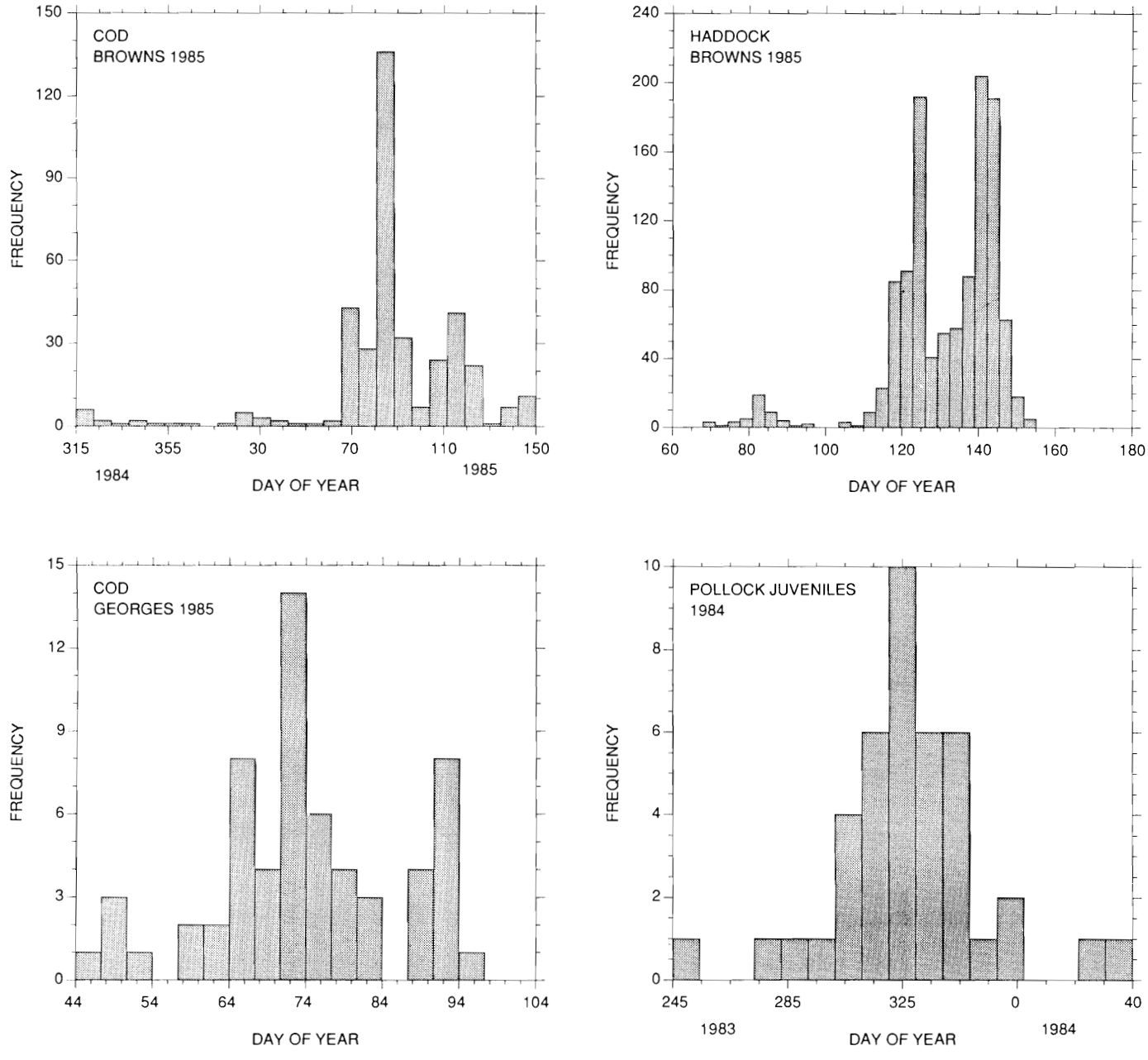


FIG. 9. Hatch date distributions of cod, haddock, and pollock derived from examination of otolith microstructure. Cod and haddock data were derived from larvae collected in all 1985 cruises; pollock data were derived from examination of a single collection of juvenile fish. Cod data have been further classified into Browns Bank and Georges Bank collections.

formation. In practice, the assumption is even more stringent, since the distinction between true daily increment formation and its correct interpretation is irrelevant. Daily increment counts appeared to provide accurate and precise reflections of age of cod and haddock (somewhat less so for pollock) in this and other studies (Radtke and Waiwood 1980; Bergstad 1984; Dale 1984). However, two potentially serious sources of error were identified: resolution-limited visibility of narrow increments and a zone characterized by prominent subdaily increments.

The resolution-associated underestimates of age noted in cod and haddock otoliths ($<1-2$ d) were considered acceptable in this study, and would probably be so in most other studies. However, it is important to note that resolution-associated error is correlated with larval growth rate (Geffen 1982; Campana et al. 1987; Jones and Brothers 1987); hence more serious errors may result if increment counts remain uncorrected for resolution bias in slower-growing populations. An extreme example of such a problem may have been evident in the exceptionally poor increment clarity of both the laboratory-reared and the field-collected pollock larvae. Support for this statement comes from the fact that increment clarity increased with the broader increment widths characteristic of older pollock larvae and juveniles. A feature inconsistent with this argument was the poor increment visibility of the laboratory-reared pollock in which increment widths were comparable to those of laboratory-reared cod. Whatever the causal mechanism, pollock otoliths were unquestionably difficult to interpret

during their larval stage; caution is recommended to those who would study them further.

The presence of a zone of prominent, and potentially confusing, subdaily increments was a second possible source of error in the interpretation of cod and haddock microstructure. Although associated with a region of rapidly increasing increment widths, there was no immediately apparent reason for the existence of such a region. The age and size at formation of the zone was not consistent with the size reported for the life history transition from a pelagic to a demersal existence (Koeller et al. 1986). Nevertheless, the subdaily increments observed here were among the most prominent yet observed by the author.

The error contributed by resolution effects and subdaily increments was minimal in this study. The assumption that increment counts, whether of lapilli or sagittae, provide an accurate, precise index of age in cod and haddock larvae was supported. To the extent that environmental variables influence larval and otolith growth rate, this assumption may not hold for other populations, and requires further testing in the case of pollock. Resolution-limited visibility of daily growth increments has now been documented in a number of temperate pelagic larval populations and species (Campana et al. 1987; Jones and Brothers 1987; this study), suggesting that it may be a widespread phenomenon among slow-growing larvae. Since resolution effects intoduce bias, and not just random error, into age estimates, routine testing for its presence is warranted.

Use of otolith microstructure for growth back-calculation purposes assumes correspondence between otolith and fish size. Linear relationships between otolith diameter and larval length were demonstrated for all three gadid species and both otolith types (lapilli, sagittae) after the appropriate data transformation. On a gross scale, these relationships were similar among cruises, years, and areas. More detailed analysis revealed significant differences among samples, emanating from two sources. The first source of variation primarily influenced the diameter of small otoliths (<30 μm diameter), through an expected association with the diameter of the hatch check. However, systematic variations in hatch check diameter were negatively correlated with temperature, resulting in smaller hatch check diameters later in the spring. A similar relationship has been reported for salmonids (Neilson et al. 1985), and is likely due to a seasonal shift in larval size and egg diameter at the time of hatch (Knutsen and Tilseth 1985; Markle and Frost 1985). Given the small magnitude of the slope of the relationship, seasonal shifts in hatch check diameter would not become evident in back-calculation applications except in analyses of newly hatched larvae collected over intervals of several months. A more significant source of error was apparent in the different otolith − larva length relationships among samples. Tests for commonality of slope and (or) intercept were inconclusive in determining if one or both parameters differed among samples. Therefore, there are three possible sources of the variation. Genetic differences among cohorts is, of course, one possibility. A second is a relationship between the otolith diameter − larval length regression slope and larval growth rate, as has been demonstrated elsewhere (Secor and Dean 1989). A third possibility is differential larval shrinkage associated with handling and (or) environmental differences at the time of preservation (Theilacker 1980). Whatever the mechanism, significant differences in otolith−larva relationships among samples could bias inferences based upon back-calculation, depending upon the detail of the analysis (West and Larkin 1987). As with resolution effects, an environmental component is likely to be causally linked to this problem.

Early life history inferences presented here were of a scale unaffected by the caveats noted above. Estimated dates of hatch for cod and haddock should be accurate to several days, while the more problematical pollock otoliths should reflect true hatch dates to within 2 weeks. Hatch date distributions for cod (March−April) and haddock (May) are consistent with reports based upon the Scotian Shelf Ichthyoplankton Program (SSIP) (O'Boyle et al. 1984; Gagné and O'Boyle 1984) if allowance is made for the 2- to 3-week duration of the egg stage (Laurence and Rogers 1976). The hatch date distribution for the 1985 year class of cod on Georges Bank in this study was nearly identical with that reported for the 1981 year class by Bolz and Lough (1983). The 1- to 2-month interval between modal hatch dates in cod and haddock was also consistent with other studies (O'Boyle et al. 1984; Gagné and O'Boyle 1984; Bolz and Lough 1983). As might be expected given the temperature differences on the two banks (Campana and Hurley 1989), cod hatched significantly earlier on Georges Bank than on Browns Bank. However, a small number of cod were spawned in the fall on the Scotian Shelf, while no such fall spawning was apparent on Georges Bank. Fall spawning for cod was also documented in the SSIP collections (O'Boyle et al. 1984; Gagné and O'Boyle 1984).

In contrast to cod and haddock, pollock hatch dates were entirely restricted to the fall (November). Given a 1-week egg stage (McGlade 1983), pollock spawning would have occurred in mid-November; such a date is consistent with the November−December spawning date reported elsewhere (Bigelow and Schroeder 1953; McGlade 1983; O'Boyle et al. 1984).

In a separate study, Campana and Hurley (1989) developed a model for cod and haddock larvae that predicted growth of larvae in the Gulf of Maine and elsewhere. The model assumed logistic growth and a parabolic relationship between daily temperature and absolute daily growth rate. There were too few data to fit the model to pollock larvae; however, it is likely that an age- and temperature-mediated growth model would have provided greater predictive powers for pollock than the exponential model fitted here. At a temperature consistent with observed winter temperatures in the Gulf of Maine (5°C), cod and haddock larval growth was comparable to that observed for pollock. There are no other published records of larval pollock growth with which to compare these data.

The assumptions forming the basis for these microstructure-based, early life history inferences were largely met. However, deviations were noted that could influence other, more detailed, applications, particularly those associated with back-calculated growth and slow-growing pelagic larvae. None of the deviations appear to be insurmountable and, in most cases, will simply require documentation. Where quantification is required (e.g., resolution effects), the appropriate procedures either already exist or are amenable to development (e.g., Campana et al. 1987). Given the influential role of the environment in its effect upon these assumptions, it is likely that different habitats will be characterized by different potential levels of precision and accuracy in the application of otolith microstructure examination.

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