Abstract.–We examined the relationship between otolith size and larval standard length (SL) at hatching for Atlantic cod, *Gadus morhua*, on the Scotian Shelf. We found a weak correlation between SL and area-based and radius-based measures of size of both lapillar and sagittal otoliths. Correlations of SL with the area of the lapillus were strongest. However, the predictive ability of all relationships was low. For example, the range of predicted SL at hatching of larvae with lapilli of average area included more than 90% of observed SLs in newly hatched larvae from the Scotian Shelf collected over two spawning seasons. These results suggest that otolith-based attempts to backcalculate the size of cod larvae may be prone to substantial error if sizes of particularly young larvae are estimated. We recommend that, where possible, stock- and season-specific estimates of the relationship between the area of the lapillus and larval size at hatching be used in back-calculation techniques.

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The relation between otolith size and larval size at hatching for Atlantic cod, *Gadus morhua**

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The variation in year-class strength in fish populations has profound implications for our ability to manage stocks wisely. Recently, considerable effort has been focused on trying to understand why the few individuals that survive do so, rather than why the majority die (Crowder et al., 1992). This approach, which relies inherently on characterizing traits in individual fish, has been widely applied in both marine and freshwater studies (Herman et al., 1996; Rice et al., 1997 for example). The philosophy behind the approach is that by understanding how survivors differ from those that die, one may expose the mechanisms that regulate recruitment (Fritz et al., 1990).

We used this approach to explore recruitment mechanisms in Atlantic cod, *Gadus morhua*, on the Scotian Shelf. In this area, cod spawning is bimodal, beginning in late October and continuing to the following April, with peaks in December and March (Miller et al., 1995). Recent studies have suggested the importance of small-scale physical oceanographic features, such as gyres and fronts, for larval survival (Taggart et al., 1996; Lochmann et al., 1997). Abundant populations of copepods, particularly *Pseudocalanus* and *Paracalanus*, co-occur with cod larvae (McLaren and Avendaño, 1995) and support rapid larval growth. By following birth-date cohorts through time and repeatedly estimating the distribution of phenotypic and genotypic traits in the cohort, we hoped to quantify whether survivors were different functionally from the majority that died, or whether they were simply lucky (Miller, 1997).

Genetic evidence suggests that cod larvae collected on the Scotian Shelf originate from distinct spawning events (Ruzzante et al., 1996). However, Ruzzante et al. (1996) have shown that the genetic structure within the population remains stable over time. Meekan and Fortier (1996) repeatedly sampled two autumn-spawned cohorts of Scotian Shelf cod, following each for approximately six months. The pattern of survival for the two cohorts differed. In 1991–92, the growth rate distribution of survivors differed little from the growth distribution of the cohort from which they were drawn. In contrast, in 1992–93, Meekan and Fortier (1996) found evidence of strong selection

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for faster growing fish. Moreover, after comparing otolith sizes at hatching, Meekan and Fortier (1996) suggested that the potential for faster growth expressed by the survivors may have been present at hatching.

Our ability to detect examples of phenotypic selection evidenced above depends on our ability to quantify the distribution of traits in the entire cohort and to hindcast the distribution of traits in the survivors (Miller, 1997). For much of the research discussed above, and for many other individual-based studies, otolith microstructural analysis is used to detect phenotypic selection. However, to apply this approach, three requirements must be satisfied (Francis, 1990): 1) primary increments must be deposited at a known and consistent rate; 2) there must be a quantifiable relationship between growth and the width of increment rings; and 3) the initial otolith size, defined by the presence of a check mark, must be related to the size of the fish at the formation of the check.

For cod, the regularity of increment deposition has been verified and validated (Bergstad, 1984; Radtke, 1984; and see Geffen, 1995, for a recent example). Thus, the first condition for back calculation has been satisfied in cod. However, there remains considerable uncertainty over the status of the remaining two conditions. The relationship between somatic and otolith growth in cod is unclear (see Geffen, 1995, and Meekan, 1997, for opposing views). The lack of a clear relationship between rates of somatic and otolith growth may result from the natural variability among and within many cod populations (Brander, 1994; Chambers, 1997). Typcially, cod larvae grow at highly variable rates, and somatic and otolith growth may become disassociated (Suthers et al., 1989; Campana and Hurley, 1989; Geffen, 1995). Concerns over the validity of the assumed relationship between fish and otolith size at hatching also arises because of inter- and intrapopulation variation. Considerable variation has been reported in larval size at hatching both within and among populations (Bolz and Lough, 1983; Bergstad, 1984; Radtke, 1984; Knutsen and Tilseth, 1985; Miller et al., 1995). Currently, no clear link between otolith size and larval size at hatching has been established for any population.

The objective of this paper is to examine the relationship between otolith size at hatching and larval size at hatching for cod. Specifically, we address whether otolith size at hatching is significantly correlated with larval size at hatching, and whether all otoliths provide an equally accurate and precise estimate of larval size at hatching. We use data collected for cod on the Scotian shelf collected between 1991–93 to address these questions.

Methods

Sampling was carried out during 29 cruises on the Scotian Shelf between March 1991 and May 1993 (Fig. 1). O'Boyle et al. (1984) have given a general description of the Scotian Shelf system. Full details of the sampling method are given by Miller et al. (1995). We summarize the general sampling design here and provide additional details that relate to the specific objectives of this study.

Twenty six cruises were designed to provide broad-scale information on temporal and spatial distributions and abundance of cod eggs, larvae, and juveniles (Fig. 1). We sampled a rectangular grid of 45

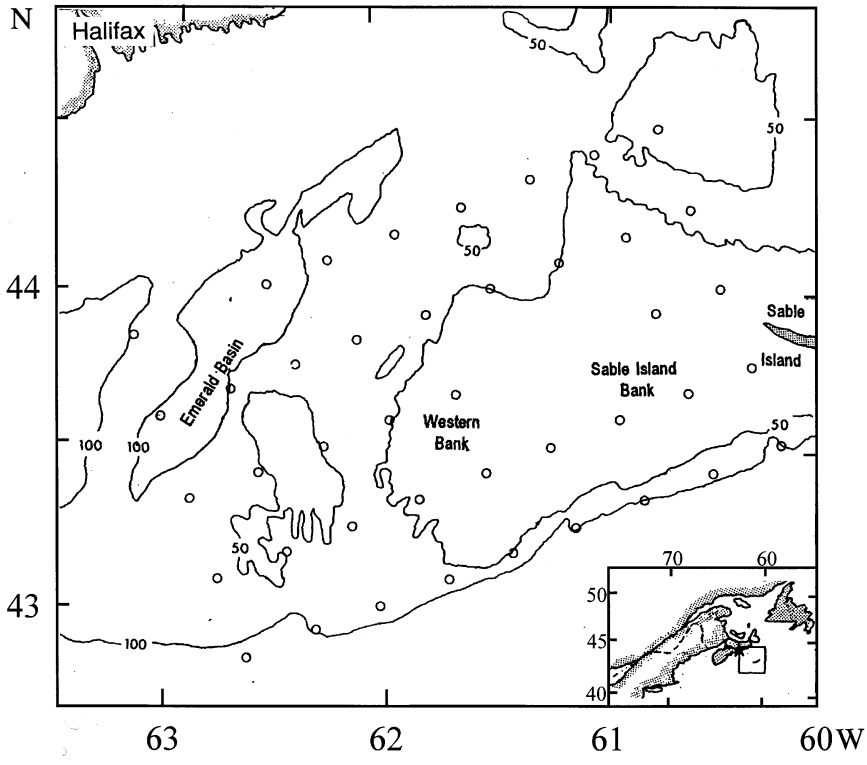

Figure 1

Map of Scotian Shelf showing the area of sampling locations. Shown on the figure are the 50- and 100-m depth contours, the principal sampling locations within the 45-station grid (open circles), and the location of Halifax, NS, Canada, for reference.

stations at roughly monthly intervals using either paired 0.61-m bongo nets fitted with 333-µm mesh nets, an 8 + 2 m rectangular mid-water trawl (RMT) fitted with 1600-µm and 333-µm mesh nets, or a paired 1.4 m^2 rectangular frame net, fitted with 333-µm mesh nets. Depth information for both the bongo and frame net was estimated from cable angles and lengths deployed. The RMT was fully equipped and provided continuous, real time depth, temperature, salinity, and volume filtered data. The station exhibiting the highest concentration of cod larvae was resampled with a BIONESS sampler equipped with ten 1-m^2, 333-µm mesh nets, that was deployed to sample discrete 5-m depth strata in the upper 25 m of the water column and 10-m depth strata at deeper depths. Three of the 29 cruises were designed to track a patch of eggs and larvae over smaller spatial scales for up to 20 days in order to track how traits changed over time. On these cruises we deployed principally a BIONESS sampler and bongo nets. However, because we were attempting to sample continuously from the same patch of water, stations were distributed irregularly in space.

All net samples were sorted and cod eggs were removed on board ship. Late-stage eggs that appeared healthy and undamaged by the collection process were videotaped under a dissecting microscope at 6–50× magnification. Individual eggs were incubated separately on a 12-h light:12-h dark cycle and at near-ambient temperature. Light from blue incandescent bulbs mimicked the light environment at depth. Nursery temperatures were recorded daily. All eggs from the same cruise were incubated at the same temperature. However, because sea temperatures varied across the sampling grid, and with depth, there were unavoidable differences between incubation and ambient temperatures for individual eggs. Vials were checked every 12 hours for hatching. When a larva hatched, it was immediately videotaped and stored in liquid nitrogen prior to otolith extraction and analysis.

In the laboratory, lapillar and sagittal otoliths were removed from larvae and mounted in cyanoacrylic cement. In most larvae we could remove and classify successfully all four otoliths. Otoliths were examined under bright field illumination under a compound microscope at 60–1000× magnification. Oil immersion was required for the higher magnifications.

Videotape recordings and otolith images were analyzed in the laboratory by using an image analysis system (Optimas v3.11, Bioscan Corporation, Seattle WA). We staged each egg according to Thompson and Riley's (1981) system. Egg diameters were calculated from three digitized points on the circumferences of eggs. From these points the diameter was calculated as

$$Diameter = \frac{abc}{4\sqrt{s(s-a)(s-b)(s-c)}},$$

where a, b, and c = the lengths of the chords connecting the three points; and
$s = 2(a + b + c)$.

Larvae that hatched from these eggs were measured to standard length (SL). Only undamaged otoliths were analyzed. Several measures were taken to describe otolith size. At this early stage, otoliths were essentially spherical in cross section. We measured the cross-sectioned area of both lapillar and sagittal otoliths. We also measured the radius of the otolith at hatching because this is the most common measurement used when estimating larval hatching sizes from otolith data.

Analysis of the data collected depended upon the purpose to which the analysis was being put. For univariate analyses to determine seasonal trends in a trait, data were aggregated to provide a mean value for each deployment before analysis. This approach reflects the sampling design employed in the field, and thus the deployment is the appropriate sampling unit. However, for bivariate analyses to determine the correlation among measures of otolith size and between otolith size and fish size, the individual fish is the appropriate sampling unit, and thus these analyses were conducted at the individual level.

Results

We identified and incubated 650 cod eggs from April 1991 to May 1993. Of this total, 259 (39.9%) successfully hatched. Otoliths from a random sample of 73 of these larvae were used in our analyses. We obtained reliable measurements from both lapilli on 56 larvae (76.7%) and from both sagittae for 59 (80.1%) larvae. The distribution of data, by month and year, is given in Table 1.

We examined the correlation structure in the data for area of otolith and radius of otolith at hatching. Estimates of otolith area were correlated among otolith types, but there were no significant correlations among otoliths from the same side of the body (Fig. 2). Moreover, the correlation among lapilli was greater than that for sagittae (Fig. 2). An identical pattern was found with respect to radius of otolith at hatching (Fig. 3).

We regressed each measure of otolith size on larval size at hatching, using only otoliths from the left side of the body. The area of the lapillus (LA) and SL at hatching were significantly and positively related (Fig 4A). Overall, longer larvae have bigger lapilli. The 95% CIs around the predicted mean were nar-

Table 1

Mean size (±SD) and number of newly hatched cod larvae from the Scotian Shelf providing data for otolith analysis by month and year. Otolith mean and SDs are calculated by using estimates for both otoliths of the specified type within each fish. Shown for each entry are the mean (upper number), SD (middle number in parentheses), and number of fish providing data for analyses (lower number).

	1991–92				1992–93			
Measurement	Nov	Dec	Jan	Mar	Oct	Dec	Mar	Total
Egg diameter (mm)	1.35 (0.1) 43	1.45 (0.07) 37	1.35 (0.05) 11	1.51 (0.1) 2	1.38 (0.06) 91	1.51 (0.06) 40	1.59 (0.09) 35	1.47 (0.1) 259
SL at hatching (mm)	4.31 (0.2) 43	4.43 (0.3) 37	5.04 (0.2) 11	5.34 (0.3) 2	4.03 (0.3) 91	4.52 (0.3) 40	5.03 (0.3) 35	4.38 (0.5) 259
Lapillar area (μm^2)	493.0 (113.9) 6	529.5 (66.1) 7	696.49 (98.5) 5	732 1	360.69 (74.0) 10	562.51 (113.2) 8	584.48 (90.5) 19	537.34 (131.6) 56
Lapillar radius at hatching (μm)	13.6 (1.4) 6	14.12 (0.8) 7	15.87 (1.1) 5	15.87 (0.9) 1	11.71 (1.2) 10	14.80 (1.0) 8	14.74 (1.6) 19	14.13 56
Sagittal area (μm^2)	191.3 (69.6) 6	270.29 (83.1) 11	369.12 (108.6) 5	360.57 (50.9) 1	227.25 (84.9) 10	333.37 (64.1) 8	280.71 (85.9) 18	276.6 59
Sagittal radius at hatching (μm)	8.79 (1.29) 6	10.39 (1.4) 11	11.98 (1.7) 5	11.85 (1.2) 1	9.55 (1.5) 10	11.32 (1.3) 8	10.64 (1.5) 19	10.45 60

row. For a lapillus of average area, the predicted mean larval SL at hatching was 4.55 mm. The 95% CIs around this value were 4.4 mm < SL < 4.66 mm, a range of 0.2 mm. However, in our application we were more interested in the 95% CIs of an individual prediction. The range in these values was much wider, 3.66 mm < SL < 5.41 mm., a range of 1.75 mm. We conducted a similar analysis for the radius of the lapillus at hatching (LR, Fig 4B), which was significantly and positively related to SL at hatching. Overall, longer larvae had wide lapilli at hatching. As with the results for the total area of the lapillus, the 95% CIs for larval SL predicted for a lapillus of average radius were narrow. For a lapillus of average radius at hatching (14.15 μm), the associated 95% CIs of the mean were 4.44 < SL < 4.69 mm, a range of 0.25 mm. However, the prediction is less precise for individual back calculations for the associated 95% CIs of the individual prediction were 3.72 < SL < 5.49 mm, a range of 1.77 mm.

We conducted a similar regression analysis for the area and radius of the sagittae and SL at hatching. There were significant linear relationships for both measures of otolith size and SL at hatching (Fig. 5). For an average sagittal area of 276 μm, the predicted SL at hatching was the same as that for the lapillus. The 95% CIs for the population average were 4.38 mm < SL < 4.75, a range of 0.37 mm. The wider confidence intervals for the population mean for the sagittal measurements compared with the lapillar measurements reflected the lower coefficient of determination (r^2) of the regression. Moreover, the 95% CIs of an individual prediction, based upon sagittal area, were also wider than those for lapillus-based predictions (3.48 < SL < 5.64, a range of 2.16 mm). Similar patterns were observed for the regressions for sagittal radius at hatching (Fig. 5B).

We examined the potential for egg size and temperature to increase the predictive power of the relationships. We performed these analyses on data aggregated to the deployment level. Standard length at hatching was positively related to egg size: SL = 0.656 (±0.46) + 2.55 (±0.31) × egg diameter, n = 128, r^2 = 0.345, P = 0.0001. To explore the potential for egg size to explain additional variation in otolith-size and SL-at-hatching models, we regressed the residuals from the relationship of egg diameter to SL on several measures of otolith size. If egg size explains additional variation, independent of SL at hatching, we would expect to see a significant regression statistic. The residuals were significantly related to the area and the radius at hatching of the

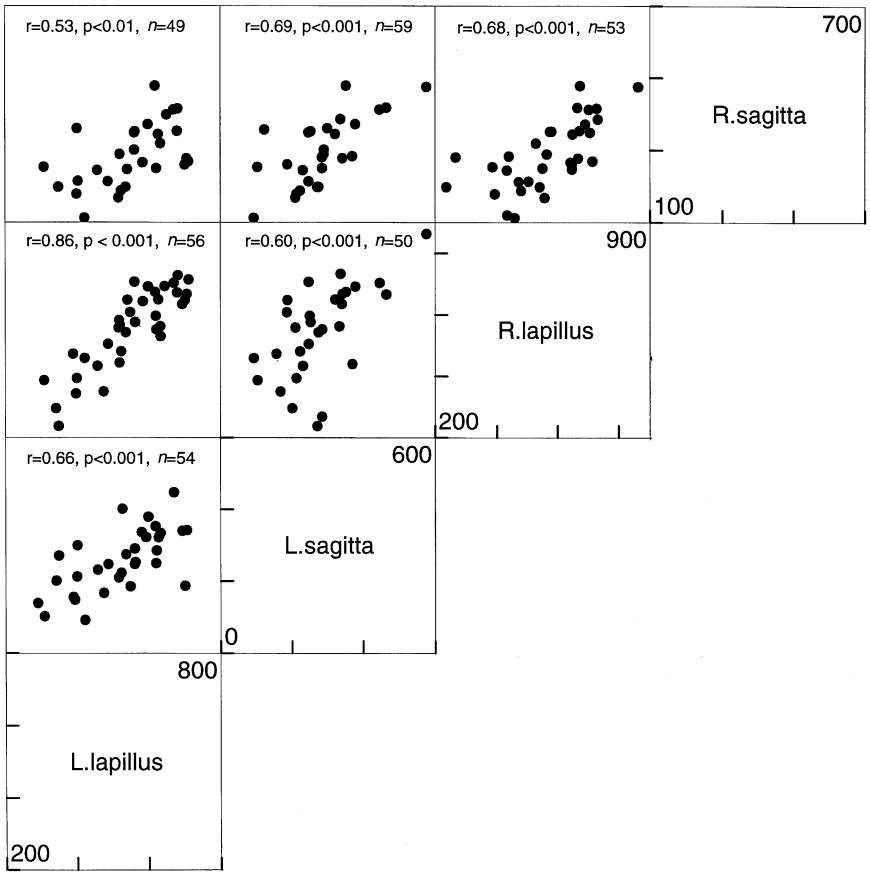

Figure 2

Scatter plots of individual measures of otolith area (μm^2) for newly hatched cod larvae collected on the Scotian Shelf. Correlation coefficients (r) for each relationship are given in each panel.

lapilli (Fig. 6). However, the residuals were not significantly related to either measure for sagittae.

Standard length (SL) at hatching was negatively related to sea temperature at collection: $SL = 5.26 (\pm 0.07) - 0.939(\pm 0.007) \times \text{temp}$, $n = 44$, $r^2 = 0.79$, $P = 0.001$. To explore the potential relationship between otolith size and temperature, we regressed our most predictive estimate of otolith size, lapillar area, against the residuals from the SL-temperature relationship. There was no clear relation between temperature residual and lapillar area (Fig. 7).

Discussion

Otoliths can be used to infer the standard length of cod larvae at hatching. However, our data suggest that the precision with which such inferences can be drawn may not be sufficient to permit accurate comparisons of the size distribution at hatching between survivors and the population at large. On the Scotian Shelf newly hatched cod larvae varied between 2.4 and 6.1 mm SL (Miller et al., 1995). The best regression relationship we developed in our study related SL to area of the lapillus, and explained 35% of the variation in the data. Accordingly, 65% of the variation remained unexplained. The regressions we developed suggest that the 95% confidence intervals of individual back-calculated size at hatching for a fish are wide. Predicted SL for larvae with average-size lapilli ranged from 3.66 to 5.41 mm. This covers fully 48.7% of the total range in initial sizes at hatching observed in cod larvae from the Scotian Shelf. More strikingly, based on estimates of mean and variation of SL given by Miller et al. (1995), this range includes 91% of all newly hatched cod larvae on the Scotian Shelf. Back calculations from lapillar otoliths larger or smaller than average size will be even more imprecise. Thus, we conclude that estimates of initial size in cod larvae are unlikely to be sufficiently pre-

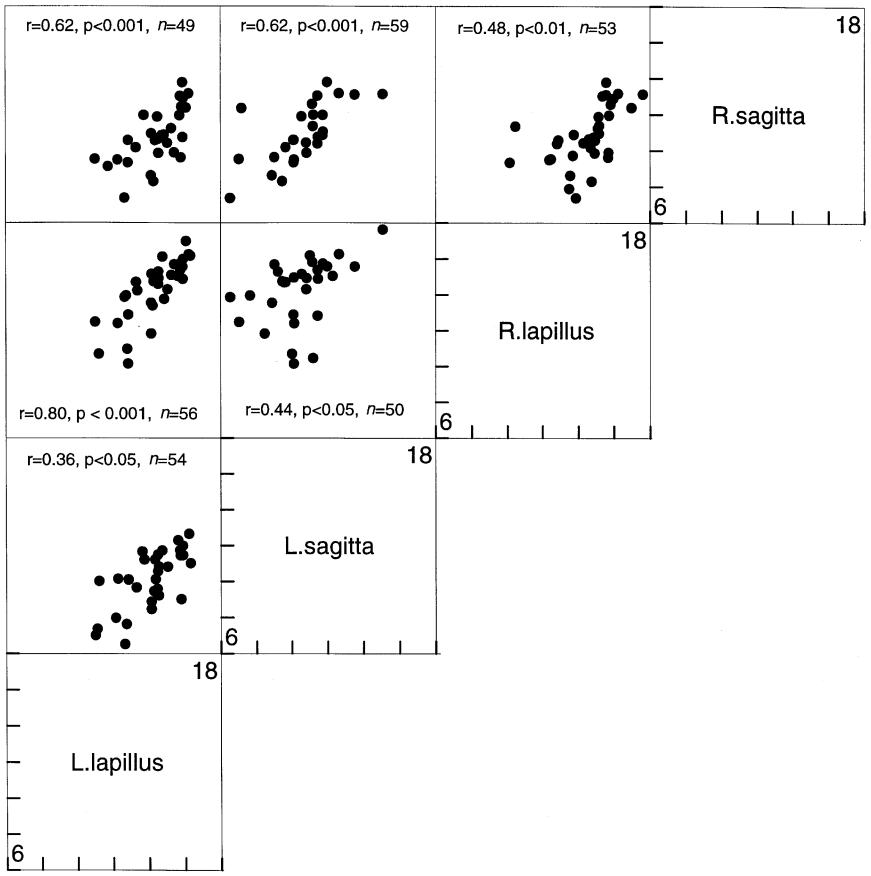

Figure 3

Scatter plots of individual measures of otolith diameter (mm) at hatching for newly hatched cod larvae collected on the Scotian Shelf. Correlation coefficients (*r*) and significance for each relationship are given in each panel.

cise to detect anything other than substantial differences in hatching size among the survivors and the initial cohort.

Meekan and Fortier (1996) reported evidence that surviving cod larvae on the Scotian Shelf in 1992–93 were significantly different from the cohort from which they originated. In contrast, survivors did not differ from the cohort at large in 1991–92. Meekan and Fortier (1996) suggested that the change in radius at hatching that they observed in 1992–93 was evidence of selection for faster growing larvae in that cohort. Meekan and Fortier's suggestion, as it relates to the relative sizes of otoliths in the survivors and the initial cohort, is indisputable. Our findings that the size of a larva and its otoliths are weakly correlated do not allow us to reject the notion that survivors may have differed in size at hatching from the overall cohort. Our results suggest an additional explanation. We report here a significant relationship between otolith size and the residual from the predicted relationship between egg and larval sizes. Larvae that hatch from relatively larger eggs, which have relatively larger yolks, have larger otoliths. Hence, we agree with the Meekan and Fortier's (1996) suggestion, but we would further hypothesize that the difference observed may have been caused by variation in egg size rather than by variation in larval size at hatching directly. If correct, we suggest that the greater amount of yolk in larger eggs enhanced initial larval growth and survival. An understanding of the actual mechanism responsible for these faster growing larvae will require additional analyses.

Our results suggest that attempts to backcalculate size of cod larvae will be most successful if they are based on measurements from the lapillus. Although larval SL at hatching was significantly related to all measures of otolith size, relationships involving the lapillus explained more variation than corresponding relationships involving the sagitta. Moreover, regressions involving the projected area of the lapil-

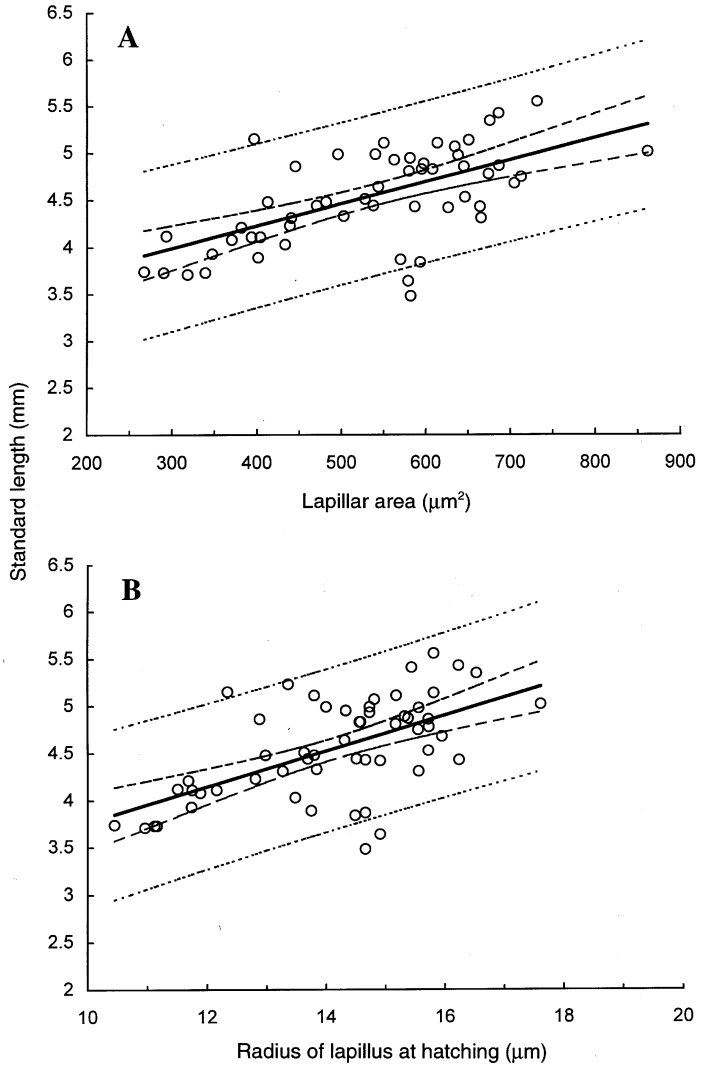

Figure 4

Relation between standard length (SL) at hatching of individual larvae and (**A**) the lapillar area (LA), and (**B**) the lapillar radius at hatching (LR) for newly hatched cod larvae on the Scotian Shelf. Shown on each plot are the predicted linear relationships and 95% confidence intervals of the mean and of individual predictions. Regression relationships are $LA = 3.295\ (\pm 0.24) + 0.0023\ (\pm 0.0004) \times SL$, $n = 54$, $r^2 = 0.35$, $P = 0.0001$; $LR = 1.898\ (\pm 0.51) + 0.188\ (\pm 0.036) \times SL$, $n = 54$, $r^2 = 0.35$, $P = 0.0001$.

lus were more accurate than those involving the radius of the lapillus at hatching. We conclude from these findings that attempts to hindcast size at hatching in cod should rely on measurements taken from the lapillus and, where possible, should use the cross-sectional area of the otolith as the measure of otolith size. It has been recognized that cod lapilli are larger initially than sagittae, but that sagittae increase in size more rapidly (Bergstad, 1984; Radtke, 1984; Campana and Hurley, 1989). Lapilli remain larger than sagittae for up to 25 days. As a result, back calculations involving cod older than 25 d or larger than 6–8 mm have been based on sagittae instead of lapilli. However, the relative sizes of the otoliths at their core remain unaltered by subsequent growth dynamics. Hence, we caution that, even though the sagittae in these larger and older fish are larger absolutely than the lapilli, the precision of estimates of initial size at hatching will be most precise if the estimates are based on the size of the lapillus at hatching.

In controlled laboratory experiments, Geffen (1995) found that the otolith-size and fish-size relationship

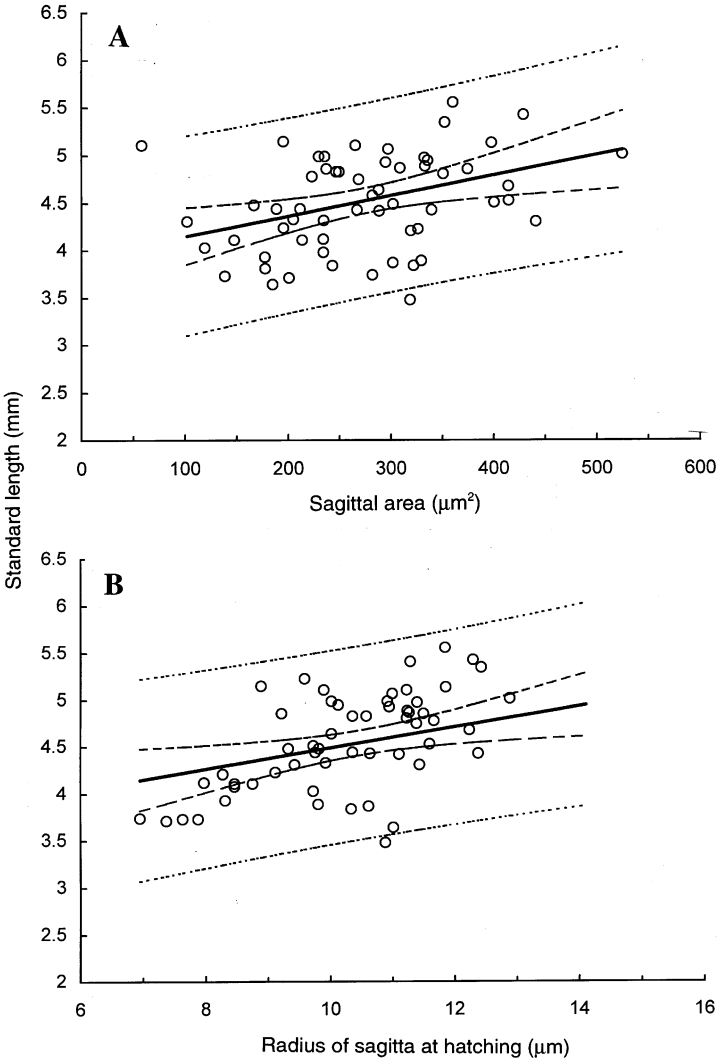

Figure 5

Relation between size at hatching of individual larvae and (**A**) the sagittal area (SA), and (**B**) the sagittal radius (SR) at hatching for newly hatched cod larvae on the Scotian Shelf. Shown on each plot are the predicted linear relationships and 95% confidence intervals of the mean and of individual predictions. Regression relationships are $SA = 4.033\ (\pm 0.21) + 0.00178\ (\pm 0.0007) \times SL$, $n = 58$, $r^2 = 0.09$, $P = 0.017$; $SR = 3.44\ (\pm 0.45) + 0.104\ (\pm 0.043) \times SL$, $n = 59$, $r^2 = 0.09$, $P = 0.018$.

could predict overall mean population growth rates extremely well but that they were unreliable predictors of individual larval growth. For example, Geffen (1995) reported that within 15 d of hatching, otolith growth and a measure of somatic growth were poorly correlated in cod larvae. If Geffen's conclusion reflects a broad pattern, her results have profound implications for any application of an individual-based backcalculation approach to cod. Recently, Meekan (1997) pointed out that Geffen's conclusions may have been affected by experimental conditions and by the use of a single mean value of larval size at hatching as the origin of the relationship between larval size and otolith size. Larval size at hatching varies substantially in cod (Knutsen and Tilseth, 1985; Miller et al., 1995), and thus Geffen's use of a single size at hatching is unrealistic and cannot be supported by the data available. Yet it is not clear what value one should use for the origin in backcalculating growth trajectories.

Our data suggest that the wide variability in the relationship between otolith size and hatching size observed in cod will likely plague attempts to

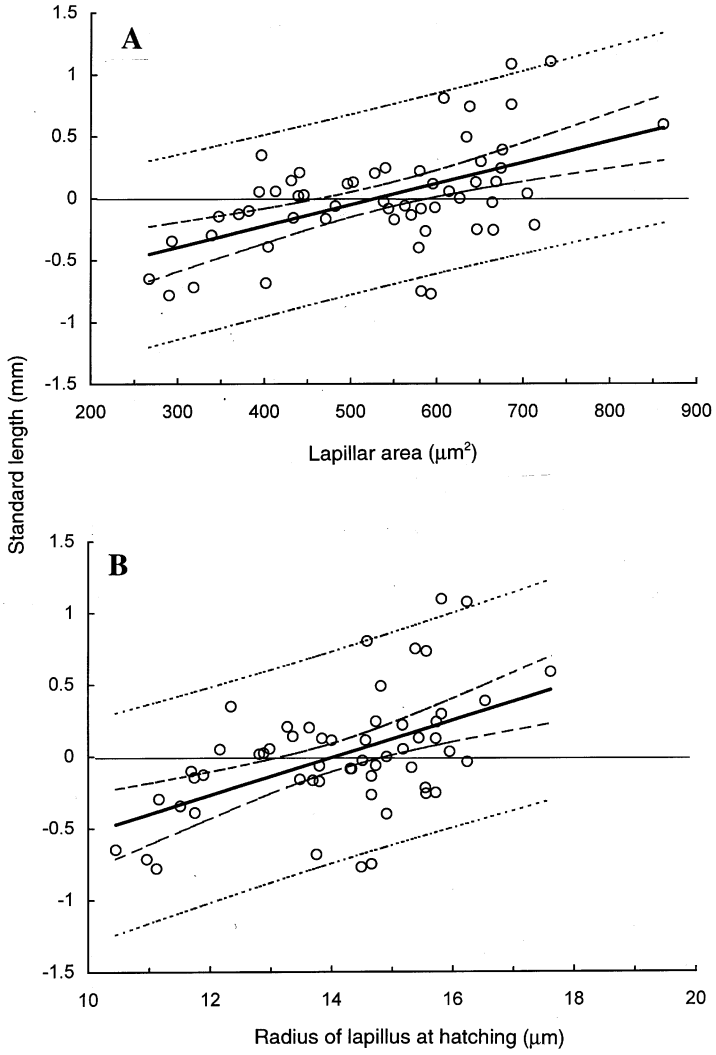

Figure 6

Relation between the residuals from the mean SL and mean egg diameter and **(A)** the lapillar area (LA) and **(B)** the lapillar radius at hatching (LR) for newly hatched cod larvae on the Scotian Shelf. Shown on each plot are the predicted linear relationships and 95% confidence intervals of the mean and of individual predictions. Regression relationships are: $Residual = 0.00162\ (\pm 0.0003) \times LA - 0.721\ (\pm 0.186)$, $n = 37$, $r^2 = 0.38$, $P = 0.0001$; $Residual = 0.126\ (\pm 0.03) \times LR - 1.633\ (\pm 0.39)$, $n = 37$, $r^2 = 0.37$, $P = 0.0001$.

backcalculate to early periods of the life history. Geffen (1995) commented on the variability in the sizes of hatchmarks on the lapilli of cod larvae. She reported estimates of otolith diameters at hatching that varied by more than twofold (13.7–28.4 µm). In Figure 8, we summarize published data on SL and lapillar diameter at hatching for a range of cod stocks. The variability evident in Figure 8 suggests that the choice of a "biological intercept" for cod is problematical (Campana, 1990); a single "best" size at hatching or otolith size at hatching clearly cannot be defined for cod. However, the data do show that an overall relationship between the mean SL at hatching and the mean diameter of lapillus exists. However, given the limited data set, the relationship is statistically insignificant ($MDL = 1.73 \times MSL + 19.54$, $r^2 = 0.306$, $n = 7$, $P > 0.05$). With these results, we recommend that extreme caution be exercised when selecting parameter estimates for use in the back calculation of size-at-age in cod.

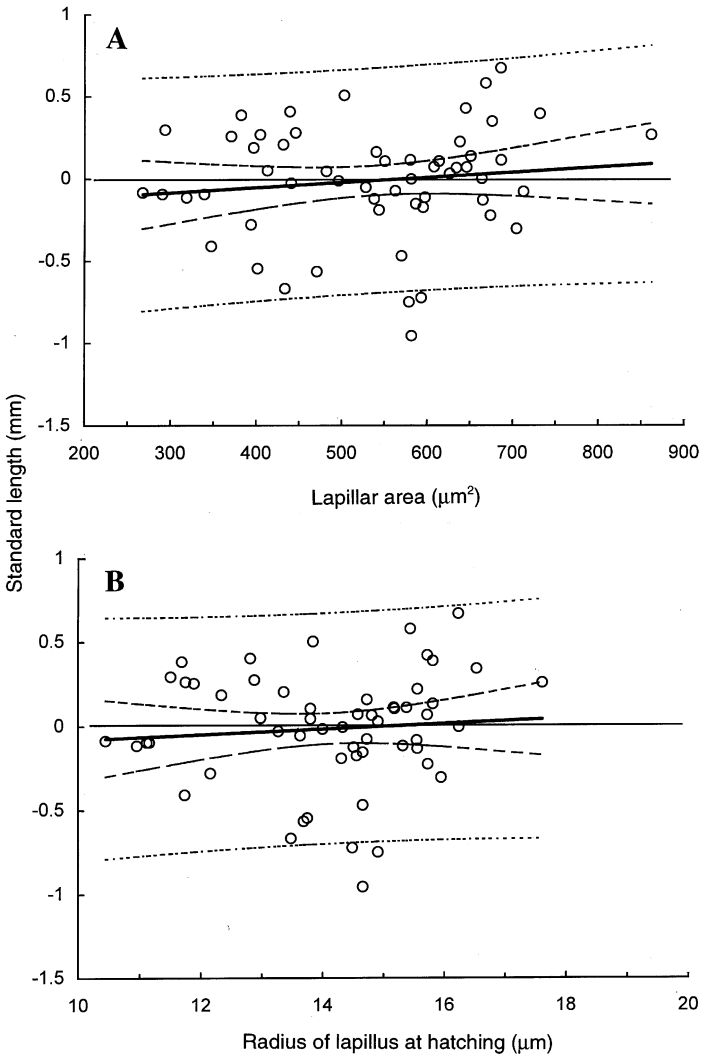

Figure 7

Relation between the residuals from mean SL and mean water temperature at collection and (**A**) the area of the lapillus (LA) and (**B**) the lapillar radius at hatching (LR) for newly hatched cod larvae on the Scotian Shelf. Shown on each plot are the predicted linear relationships and 95% confidence intervals of the mean and of individual predictions. Regression relationships are $Residual = 0.00021\ (\pm 0.00027) \times LA - 0.102\ (\pm 0.143)$, $n = 37$, $r^2 = 0.01$, $P = 0.89$; and $Residual = 0.013\ (\pm 0..21) \times LR - 0.184\ (\pm 0.28)$, $n = 37$, $r^2 = 0.001$, $P = 0.85$.

The implications from our results for studies on other species are less clear. It is important to note that one would not expect all species to exhibit the same plasticity in size at hatching, or in the relationship between fish size and otolith size at hatching. Hence, for some species there is little variation in initial size at hatching. In these species the error introduced by assuming a single, universal size at hatching is probably small. However, it is important to recognize that back-calculation techniques all assume a common origin for the family of size-at-age lines that are modeled. The methods differ only in the definition of the origin (fish size at zero otolith size, biological intercept, or otolith size at zero fish size), but all assume a single value. Indeed Campana (1990) noted that relatively little attention had been paid to the effects of variation in the intercept term of back-calculation methods; most attention had been paid to variation in the slope. However, for species that are known to vary widely in hatching size (e.g.

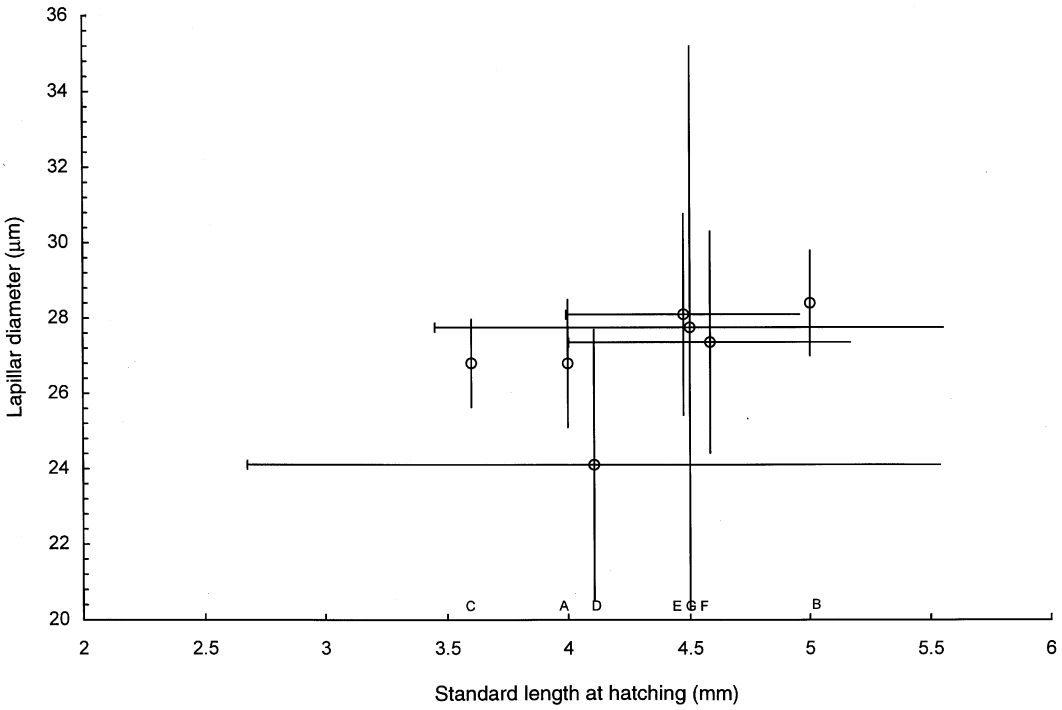

Figure 8

Relation between larval size and otolith size at hatching reported in the literature for different populations of cod. Shown for each data point are means and bivariate standard deviations (when available). The sources for individual data points are shown as letter codes above the abscissa. Codes: (**A**) Radtke (1984); (**B**) Bergstad (1984); (**C**) Radtke (1989); (**D**) Geffen (1995); (**E**) 1991–92 cohort from Meekan and Fortier (1996); (**F**) 1992–93 cohort from Meekan and Fortier (1996); and (**G**) this study. Estimates of SL at hatching for Meekan and Fortier were taken from estimates of mean hatching size for each cohort given by Miller et al. (1995).

Atlantic herring), individual variability in the intercept may be significant. We recommend that, at a minimum, stock specific values for intercepts be used if the interest is in periods of the life history shortly after hatching. Further, caution should be exercised in relating shifts in the back-calculated distribution of radii at hatching to size-selective mortality. More careful study of the relationship between otolith size and fish size in individual species is likely warranted if researchers wish to employ otolith-based back calculation (Chambers and Miller, 1995).

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