Growth variation and water mass associations of larval silver hake (*Merluccius bilinearis*) on the Scotian Shelf[1]

Jennifer A. Jeffrey and Christopher T. Taggart

Abstract: Otolith microstructure is shown to be ideal for assessing age and growth in silver hake (*Merluccius bilinearis*) larvae and is used to examine growth among individuals and cohorts. Larvae collected from Western Bank, Scotian Shelf, in September, October, and November 1997 defined three monthly cohorts identified using inferred hatch dates. Total length-at-age relations did not differ between the September and October cohorts despite substantial differences in growing degree-day (435 versus 318°C·d) and zooplankton (potential prey index) wet biomass (0.15 versus 0.27 $g \cdot m^{-3}$). Larvae collected off-bank in September exhibited a growth advantage of >0.10 $mm \cdot d^{-1}$ relative to larvae collected on-bank. Greater variability in growth rate within cohorts and among water masses implies that cohort-averaged growth and survival (based on growth) estimates can be biased by overrepresentation of a single water mass. The focus on growth variability, and its relationship to survival, should be on individuals within cohorts and not on cohort-averaged estimates. We hypothesize that growth, and perhaps survival, in silver hake larvae on the Scotian Shelf is most easily explained by variation in physical oceanographic processes.

Résumé : Nous montrons que la microstructure des otolithes est un outil idéal pour évaluer l'âge et la croissance chez les larves de merlu argenté (*Merluccius bilinearis*), et nous nous en servons pour examiner la croissance parmi les individus et les cohortes. Les larves prélevées sur le banc Occidental, sur la plate-forme Néo-Écossaise, en septembre, octobre et novembre 1997, représentaient trois cohortes mensuelles identifiées par leurs dates d'éclosion supposées. Les relations de la longueur totale selon l'âge ne différaient pas entre les cohortes de septembre et d'octobre malgré des différences substantielles dans les degrés-jour de croissance (435 c. 318°C·jour) et la biomasse humide de zooplancton (indice des proies potentielles) (0,15 c. 0,27 $g \cdot m^{-3}$). Les larves recueillies à l'extérieur du banc en septembre présentaient un avantage de croissance de >0,10 $mm \cdot jour^{-1}$ par rapport aux larves récoltées sur le banc. La plus grande variabilité du taux de croissance à l'intérieur des cohortes et entre les masses d'eau implique que les estimations de la moyenne par cohorte de la croissance et de la survie (d'après la croissance) peuvent être biaisées par la surreprésentation d'une masse d'eau. L'examen de la variabilité de la croissance, et de sa relation avec la survie, devrait porter sur les individus au sein des cohortes et pas sur les estimations des moyennes par cohorte. Nous posons que, pour les larves de merlu argenté de la plate-forme Néo-Écossaise, ce sont des variations dans les processus océanographiques physiques qui expliquent le mieux la croissance, et peut-être la survie.

[Traduit par la Rédaction]

Introduction

A principal goal of fisheries oceanography is the testing of hypotheses proposed to explain variations in the year-class strength (recruitment) of marine fishes. It was originally hypothesized that year-class strength was determined during the early life history, usually within the first year of life (Hjort 1914, 1926). Several variations on the original hypothesis have evolved (e.g., Shepherd and Cushing 1980; Iles and Sinclair 1982). Year-class strength is some function of larval survival that may be a function of growth (Houde 1987). Variation in growth (hence survival) during the prerecruitment period is thought to contribute to recruitment variation through regulation of the length of the larval stage (Houde 1987; Pepin 1991). Larger or faster growing larvae may experience a contracted larval period, reducing the time that they are subject to predation and reducing the probability of starvation associated with small size and limited motility (e.g., Miller et al. 1988; Rice et al. 1993; Meekan and Fortier 1996).

Variability in growth rate is a function of biological conditions (e.g., feeding success: Govoni et al. 1985) and oceanographic conditions (e.g., temperature and turbulence: Pepin 1991; Gallego et al. 1996). The ability to predict growth rate using these kinds of variables and their associated parameters may lead to survival and ultimately recruitment predictions from the larval stage.

Several studies have examined growth rates (inferred from size-at-age relations) that are averaged over populations or cohorts (see Rice et al. 1987). However, averaging growth rate estimates may mask relations between growth rate and environmental conditions (Rutherford and Houde 1995). Further, as size-selective mortality (starvation or predation

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J.A. Jeffrey and C.T. Taggart.[2] Department of Oceanography, Dalhousie University, Halifax, NS B3H 4J1, Canada.

[1]This paper is a GLOBEC Canada contribution.
[2]Author to whom all correspondence should be addressed.
e-mail: chris.taggart@dal.ca

related or both) acts on individuals, focussing on population- or cohort-averaged growth rates may preclude testable predictions of survivorship when growth rate is used as the predictor (Pepin 1989). Thus, the analysis of growth rate variation among individuals within well-defined cohorts may be key to resolving the processes responsible for growth rate variation and ultimately survival in larval fish (e.g., Chambers and Miller 1995; Meekan and Fortier 1996).

Growth rate variation in larval fish can be resolved using otolith microstructure (Campana and Neilson 1985). The age of an individual can be determined and individual growth rates can be calculated using somatic or otolith size-at-capture. Perhaps of greater utility is the variation in the width of daily otolith increments that may be related to daily variation in somatic growth rate and therefore provides a time series of growth variation over the life of individual larva (see review by Campana and Neilson 1985).

It is not clear that somatic and otolith growth are correlated on a day-to-day basis. Some researchers report a decoupling of the two when growth is variable (i.e., fast-growing larvae have smaller otoliths relative to body size than slow-growing larvae: Mosegaard et al. 1988; Secor et al. 1989). Others report that larval size and otolith size remain highly correlated regardless of growth rate (Dickey et al. 1997), and it is generally accepted that otolith growth is a "running average" of somatic growth (Campana and Neilson 1985). Despite uncertainties in the accuracy of back-calculation of larval size or growth rate from otolith size, questions concerning relative growth differences among larvae can be addressed given the assumption that larger otolith size-at-age corresponds to greater somatic size-at-age (Hare and Cowen 1995). For the questions that we address below, only relative comparisons of growth are important. Therefore, the precise nature of the otolith–fish size relation and the accuracy of the back-calculated larval size from otolith size is not critical.

Silver hake (*Merluccius bilinearis*) is a model species for testing growth and environment hypotheses in larvae at a variety of temporal and spatial scales, and Western Bank (Scotian Shelf) is an ideal location to conduct such tests. Mature silver hake are benthopelagic and spawn on the Scotian Shelf in summer and autumn (Scott and Scott 1988). The larvae are pelagic for 3–5 months posthatch and are generally found in the upper mixed layer (Fortier and Villeneuve 1996). There are few studies of somatic or otolith growth in silver hake larvae (>20 mm only: Nichy 1969; juveniles: Koeller et al. 1989; larvae: Buckley et al. 1993). However, Pannella (1971), in his pioneering work on otolith microstructure, concluded that silver hake deposit daily otolith increments after he estimated an average of 360 increments between the annuli of 3- and 4-year-old silver hake. Further, daily increments are confirmed for several close relatives: *Merluccius productus*, *M. angustimanus*, *M. capensis*, and *M. paradoxus* (Brothers et al. 1976; Bailey 1982; Morales-Nin 1987). Finally, Buckley et al. (1993) observed a weak inverse relation between mortality and growth in silver hake larvae in the laboratory. Thus, growth variability in the field may, in part, explain survival variability. To our knowledge, otolith microstructure has not been used to examine growth rate in larval silver hake in the field. This is surprising, as (apart from the benefits of acquiring new knowledge) protracted spawning and the persistence of eggs and larvae in regions like Western Bank over much of the autumn (O'Boyle et al. 1984; Reiss et al. 2000) provide an ideal opportunity to examine age and growth among larvae that have experienced different oceanographic conditions in time and space.

In this paper, we provide evidence that otolith microstructure is appropriate for assessing age and growth rate variation in silver hake larvae. Subsequently, we use the microstructure to test the working hypothesis that a significant proportion of growth variation among monthly cohorts and among individuals within cohorts is most simply explained by temporal and spatial variation in oceanographic conditions.

Materials and methods

Oceanographic sampling

Larvae and hydrographic data were collected in the Western Bank region (Fig. 1) between 15 and 26 September, 25 October and 10 November, and 18 November and 5 December 1997. Three monthly cohorts and two subcohorts were defined using larvae collected during the three periods. Monthly cohorts are generally defined by month of collection and specifically defined as a representative sample of larvae aged at ≤25 d at capture, with nonoverlapping hatch dates, collected in each month (September, October, and November cohorts, respectively; Table 1). Two subcohorts are defined as larvae aged between 10 and 20 d at capture and collected in each of September and October (referred to as subcohorts 1 and 2, respectively).

Larvae were collected in September and November using a 63-cm-diameter BONGO (Posgay and Marak 1980) fitted with 333-μm-mesh nets. The gear was towed in a double-oblique manner to within 5–10 m of the bottom (November) or to ~65% of the bottom depth (September). Plankton collected from one net was preserved in 5% (v/v) buffered formalin–seawater and the other in 95% (v/v) ethanol–freshwater. Larvae were collected in different strata in October using a 0.25-m^2-opening BIONESS (Sameoto et al. 1980) fitted with ten 243-μm-mesh nets. Two sets of samples were collected at each station, each set consisting of four collections from different strata and one depth-integrated collection from ~10 m above bottom to the surface (i.e., 10 nets per station, five per set). One set of collections was preserved in ethanol and the other in formalin as above. Larvae used for otolith analysis were from the samples preserved in ethanol. Volume filtered was measured for all nets using calibrated flowmeters mounted off-centre in the gear opening.

Zooplankton wet biomass ($g \cdot m^{-3}$) was used as an index of the potential prey field of the larvae and was measured using the formalin-preserved BONGO collections (September and November) and the station average of the four formalin-preserved depth-discrete BIONESS collections (October). Wet biomass was measured after fish larvae and eggs, ctenophores, and rare large plankters (amphipods, euphausiids, etc., nominally >10 mm in length) were removed to help reduce biasing the index of the potential prey field. The remaining plankton was drained on a small-mesh screen (<243 or <333 μm as required) until no longer dripping and weighed. Biomass estimates (station specific or station averaged as required) were calculated to match the various larval collections at their different scales of analyses.

Conductivity and temperature at depth were measured at each sampling station using a Seabird® Electronics SBE 25e CTD and salinity was derived and density was calculated from temperature, salinity and depth using the equation of state. Temperature time series (0.5 h resolution) were collected between 1 August and 6 December 1997 at two moorings separated by ~15 km on the crest of

Fig. 1. Bathymetric charts of Western Bank, Scotian Shelf, showing the isobaths and locations where silver hake larvae were collected in 1997 in (*a*) September, (*b*) October, and (*c*) November and (*d*) location of current meter moorings where temperature time series were collected. Solid symbols in Figs. 1*a*–1*c* represent locations included in the monthly cohorts, and open symbols represent locations where other larvae not used in otolith analyses were collected. The plus sign in Fig. 1*a* shows the location where additional larvae included in the subcohort 1 analyses were collected.

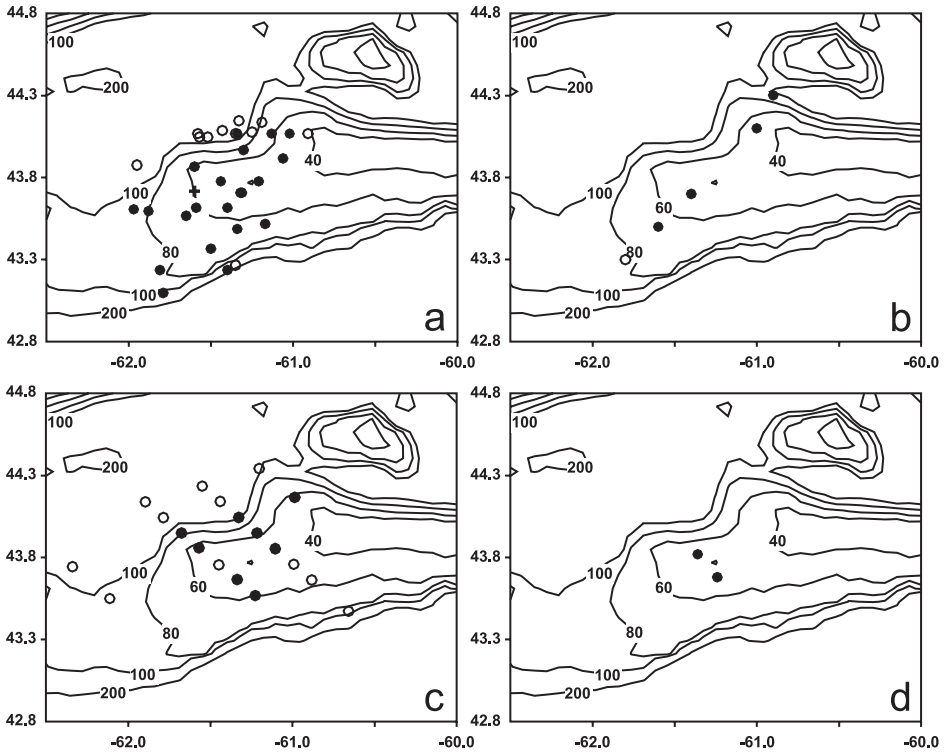


Table 1. Summary of Western Bank silver hake larvae collected, analyzed, and assigned to each monthly cohort.

Cruise	Sampling period	Estimated number of larvae available	Number of aged larvae	Number of larvae aged ≤25 d	Cohort	Inferred cohort hatch dates
Q-242	15–26 Sept.	9526 (33)	175 (23)	165 (21)	September	28 Aug. to 20 Sept.
H97-063	25 Oct. to 10 Nov.	135 (5)	128 (5)	101 (4)	October	3–25 Oct.
N97-070	18 Nov. to 5 Dec.	205 (19)	52 (10)	17 (8)	November	29 Oct. to 17 Nov.

Note: Values in parentheses represent the number of stations from which larvae were collected.

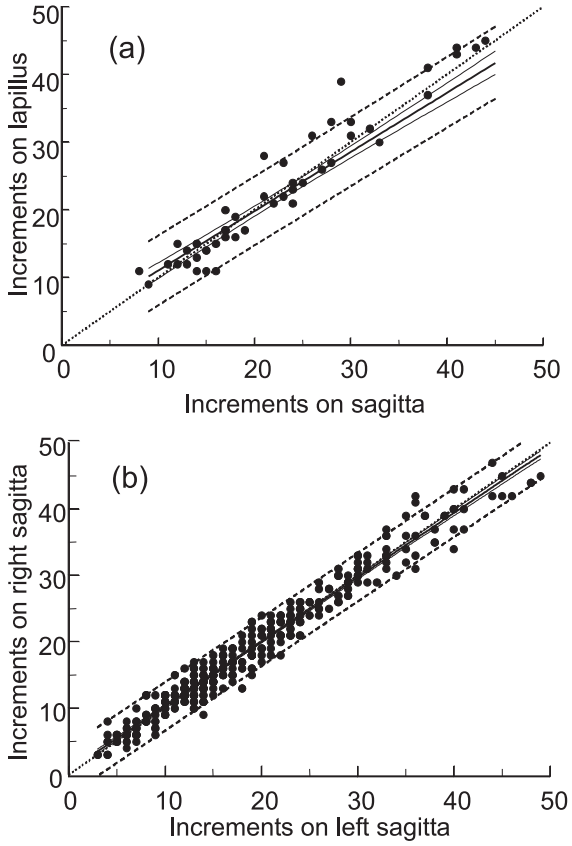
Western Bank (Fig. 1*d*). Each mooring consisted of an Interocean S4 current meter (with temperature probe) moored at 11 m depth and a temperature recorder (Vemco Inc., Dartmouth, N.S.) moored at 2 m depth. Series data were smoothed using a 25-point moving median and daily temperature estimates were calculated as the average of the daily noon (UTC) values of the four series. Growing degree-day (GDD) estimates were calculated as the running sum of the average daily temperature estimates (°C) calculated for a 25 d period beginning with the earliest inferred hatch date for each monthly cohort.

Larvae and otolith microstructure

All formalin-preserved fish larvae collected with the BONGO were removed, identified to species, and enumerated. The abundance of formalin-preserved silver hake was used to select stations and the number of ethanol-preserved larvae destined for otolith analysis. Ages (d) were obtained for 175 of the 9526 silver hake collected in September that represented 23 of the 33 stations where larvae were collected (Table 1). Stations with <25 larvae were not included in the among monthly cohort growth analyses. In November, all ethanol-preserved larvae (N = 205) were removed from collections (N = 19; Fig. 1*c*) that had larvae in the formalin-preserved sample. Poor preservation limited aging to 52 larvae collected from 10 of the 19 stations. Ethanol-preserved fish larvae collected with the BIONESS were treated as above and all silver hake from the four depth-discrete samples per station were used for otolith analysis (N = 135). Ages were obtained for 128 larvae collected in October (Table 1).

Total length (TL, ±0.1 mm) of silver hake larvae selected for otolith analysis was measured using a digital image (Sony XC-711 CCD camera and a Wild M5 dissecting microscope) and OPTIMAS® (version 5.2; Optimas Corporation 1995). TL estimates were not corrected for shrinkage in ethanol, as it is dependent on initial length and is highly variable (Fowler and Smith 1983; Jeffrey 2000). Left and right lapilli and sagittae were removed from larvae using insect needles and attached to microscope slides using cyanoacrylate glue or clear nail polish. Age was determined by counting the number of daily otolith increments at 200–1000× magnification (Wild M20) and total otolith area (OA, ±100 μm^2) was measured on a digital image taken at 40–400× magnification (Sony XC-711 CCD camera). Surface areas of individual incre-

Fig. 2. Scattergrams and least squares regressions of the number of increments (estimated age, d) for (*a*) lapilli and sagittae (lap = 2.3 + 0.88sag; r^2 = 0.93, N = 47) and (*b*) right and left sagittae (R = 0.56 + 0.97L; r^2 = 0.96, N = 382) for silver hake larvae collected from September to November 1997 on Western Bank. Solid lines show the regressions and 95% confidence bands. Dashed lines show the 95% confidence bands for the prediction for an individual. The dotted line is the 1:1 relationship.



ments were measured using a Kodak Megaplus 1.4i high-resolution digital image and SigmaScan (version 5.0.0; SPSS Inc. 1999).

There was no difference between the estimated age of randomly chosen sagittae and lapilli within individuals (Wilcoxon sign test, p = 0.44, N = 47; Fig. 2*a*). Sagittae were easier to remove and read than lapilli and are used throughout. Sagittae are considered ideal because (*i*) Pannella (1971) validated daily increment deposition on the sagittae of silver hake, (*ii*) we found that age estimates using the left and right sagittae within individuals were the same (Wilcoxon sign test, p = 0.54, N = 382; Fig. 2*b*), (*iii*) repeated blind age estimates for sagittae by the principal reader were not different (Wilcoxon sign test, p = 0.096, N = 50), (*iv*) the surface area estimates for left and right sagittae were the same (Wilcoxon sign test; p = 0.89, N = 311), and (*v*) no relation was observed between the difference in the age and the difference in surface area between sagittal pairs within individuals, suggesting that resolution of otolith increments related to otolith size is not likely a confounding factor in aging (Campana et al. 1987). Ages estimated using a subset of sagittae by the principal author and an independent experienced reader were significantly different (Wilcoxon sign test, $p < 0.01$, N = 12), although the maximum difference was 2 d. The actual age of the larvae used for interreader comparisons is unknown, and therefore, accuracy of aging cannot be assessed. As all ages were determined by the principal author, we assume that any bias is constant and we are confident that estimates from the sagittae accurately reflect the relative ages. Absolute ages and dates of initial increment formation remain uncertain, although we do not consider it critical for the focus on growth rate variation given the assumption that the time of initial increment deposition is constant for all larvae (Jenkins and Davis 1990). We assume that increment deposition begins at hatch for the estimation of relative ages. The average age and average surface area are reported for age and otolith size estimates when both sagittae were available. When only one was available, the single estimate was used.

Data analyses

The relationship between sagittal OA and larval TL was determined separately for larvae collected each month and the slopes were compared using analysis of covariance (ANCOVA). TL-at-age relations were determined for monthly cohorts (larvae ≤25 d old) when a sufficient range of ages and sizes were available and the slopes were compared using ANCOVA. Residuals of the TL-at-age relations for the September and October cohorts were examined in relation to geographic location of capture and water mass characteristics at the time of capture. Additional larvae collected from other water masses in September were examined and average somatic growth rates (ASGR, $mm \cdot d^{-1}$) and average otolith growth rates (AOGR, $\mu m \cdot d^{-1}$) were calculated for individuals aged between 10 and 20 d at capture in September and October to examine growth variation within subcohorts:

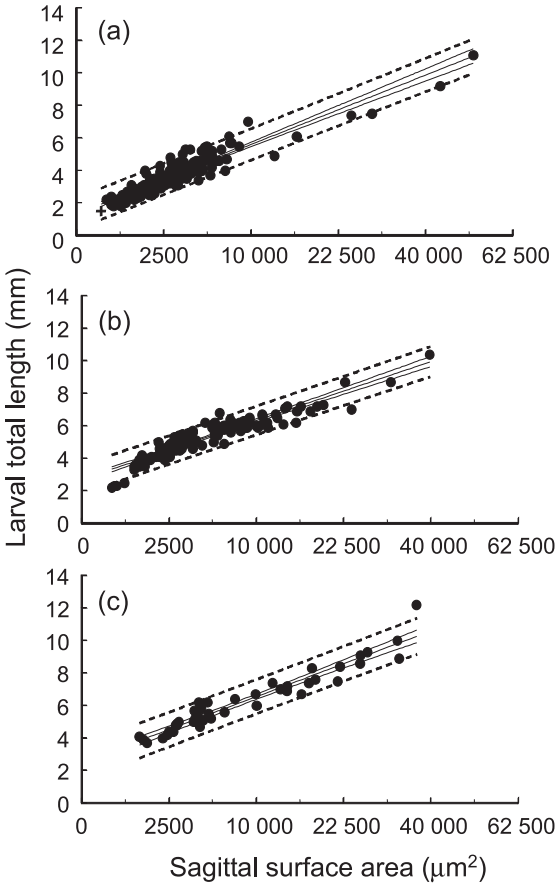
$$(1) \qquad \mathrm{ASGR} = \frac{\mathrm{TL_c} - \mathrm{TL_h}}{\mathrm{age}}$$

$$(2) \qquad \mathrm{AOGR} = \frac{\mathrm{OA_c} - \mathrm{OA_h}}{\mathrm{age}}$$

where TL_c is TL at capture and TL_h is TL at hatch as determined from the intercept of the monthly cohort-specific TL-at-age relation, and OA_c is OA at capture and OA_h is OA at hatch as estimated by substituting TL_h into the otolith–fish size relation for each monthly cohort. Thus, TL_h and OA_h varied among cohorts and were constant within cohorts. The calculation of ASGR and AOGR assumes that growth rate is constant (linear) for the period examined and that a constant somatic and otolith size-at-hatch represents hatch size for all individuals collected in the same month (cf. Geffen 1995). ASGR and AOGR were each examined in relation to a suite of physical (temperature, salinity, density, GDD, bottom depth, and depth of the surface mixed layer) and biological (zooplankton biomass, total larval concentration, larval silver hake concentration, age and hatch date) variables using bivariate and multiple least squares regression.

Otolith microstructure of 22 individuals collected from on- and off-bank water masses within subcohort 1 (September) was used to examine spatial growth variation among individuals. For these analyses the sagittal surface area ($\pm 100\ \mu m^2$) was measured at each well-defined increment (including the first prominent increment presumed to be the hatch check) when possible. TL-at-age and growth rate-at-age were back-calculated using the biological intercept method (Campana 1990) where the intercept was 1.5 mm TL and 225 μm^2 saggital surface area as recorded for the smallest larva (Fig. 3*a*). Complete TL and growth rate series were obtained for increments 3–10 and increments 4–10, respectively, for five larvae from each water mass. These series were compared among individuals from the two water masses using repeated measures multivariate analysis of variance (rmMANOVA: Chambers and Miller 1995). As the series lengths and sample sizes for the rmMANOVA were limited, the water mass specific TL-at-age and growth rate-at-age series were calculated using all 22 individuals and the slopes (using $\log_e$-transformed data) were compared

Fig. 3. Scattergrams and least squares regressions of larval TL and sagittal surface area for silver hake larvae collected in 1997 on Western Bank in (*a*) September (TL = 1.3 + 0.043(OA)$^{0.5}$; r^2 = 0.87, N = 168), (*b*) October (TL = 2.7 + 0.036(OA)$^{0.5}$; r^2 = 0.88, N = 127), and (*c*) November (TL = 2.5 + 0.040(OA)$^{0.5}$; r^2 = 0.93, N = 44). Sagittal surface area is square root transformed for the regression. The slope parameters are different among months (ANCOVA, p = 0.002). The biological intercept (Campana 1990) used for back-calculations of somatic size from otolith size is indicated by the plus sign in Fig. 3*a*. Solid lines show the regressions and 95% confidence bands. Dashed lines show the 95% confidence bands for the predictions for an individual.



(ANCOVA) between the on- and off-bank larvae. Age of divergence in average growth trajectories for on- and off-bank larvae was estimated by analyses of the back-calculated TL at hatch and TL and growth rate at each age using ANOVA (α set at 0.005 for reduced df in multiple comparisons).

All statistical analyses were performed using Systat (version 8.0; SPSS Inc. 1998) and Number Cruncher Statistical Software (Hintze 1998).

Results

Significant linear relations between TL and OA (square root transformed) were generally observed for the three monthly cohorts (Fig. 3), indicating that otolith size reflects somatic size in silver hake larvae and that OA can be used to back-calculate TL. The slopes of the relations between TL and OA were different (ANCOVA, p = 0.002) among monthly cohorts (September, 0.043; October, 0.036; November, 0.040), indicating that relations should be calculated for each cohort. All relations were monotonic with the possible exception of the October cohort where a slight decrease in slope for larvae ≥6 mm TL was apparent (Fig. 3*b*). However, fitting Gompertz, logistic, or exponential functions did not result in any improvement. For the analyses that we rely on, the OA estimates for October were further transformed to linearize the relation TL = –5.5 + 6.0 $\log_{10}$(OA$^{0.5}$; r^2 = 0.90).

Growth variation among monthly cohorts

The representative sample of larvae collected in September had inferred ages that ranged from 3 to 39 d, in October from 3 to 39 d, and in November from 10 to 47 d. Because ages were obtained for only 52 individuals in November, the larvae included in the analyses do not represent all stations in constant proportion. Larvae with ages ≤25 d were selected from each "month" to specifically define the three monthly cohorts as those with inferred hatch dates between 28 August and 20 September (September cohort, N = 165), 3 and 25 October (October cohort, N = 101), and 29 October and 17 November (November cohort, N = 17). The TL-at-age data for the November cohort are presented for comparison with the other cohorts, although the data are not used in further analyses because the sample size is small and larval size and age ranges are limited (Fig. 4). TL-at-age for the September and October cohorts were best fit with linear least squares regression (Fig. 4) and their slopes were not different (ANCOVA, p = 0.63).

All larvae in the October cohort and 52% of the larvae in the September cohort were collected during daylight (10:00–22:00 UTC for September and 10:30–21:00 UTC for October). The slopes of the TL-at-age relations for larvae caught during the day (TL = 1.7 + 0.17age; r^2 = 0.73, N = 86) and at night (TL = 1.4 + 0.19age; r^2 = 0.58, N = 79) in September were not different (ANCOVA, p = 0.35). Therefore, time of collection is ignored in the TL-at-age analyses.

The temperature time series were similar among locations and depths over the crest of Western Bank (Fig. 5). The GDD estimates were 435°C·d for the September cohort and 318°C·d for the October cohort and represent average daily temperatures of ~17 and ~13°C for larvae in each monthly cohort, respectively. The average zooplankton wet biomass for the stations included in the monthly cohort TL-at-age analyses (i.e., larvae aged ≤25 d) was 0.15 and 0.27 g·m^{-3} for September and October, respectively.

Growth variation within subcohorts

Subcohort 1 (September)

Residuals of the TL-at-age relation for the September cohort revealed a pattern among stations attributable to geographic location. For example, 79% of the larvae collected at one on-bank station had negative residuals, while >90% of the larvae collected at two off-bank stations had positive residuals. Additional larvae were examined from these and other stations to further analyze growth within subcohort 1. ASGR (N = 164) and AOGR (N = 149) were calculated for larvae aged between 10 and 20 d to prevent comparing growth rates of larvae with widely varying ages. As otoliths do not shrink with preservation, we assume that AOGR provides a better measure of growth throughout life. However,

Fig. 4. Scattergrams and least squares regressions of larval TL and age for silver hake in September and October cohorts on Western Bank. The slopes of the relations for September (solid circles; TL = 1.6 + 0.18age; r^2 = 0.65, N = 165) and October (open circles; TL = 1.7 + 0.17age; r^2 = 0.82, N = 101) are not significantly different (ANCOVA, p = 0.63). The November cohort (open triangles) is shown for visual comparison only. The solid lines show the regressions and the dotted (September) and dashed (October) lines show the 95% confidence bands for the predictions for an individual.

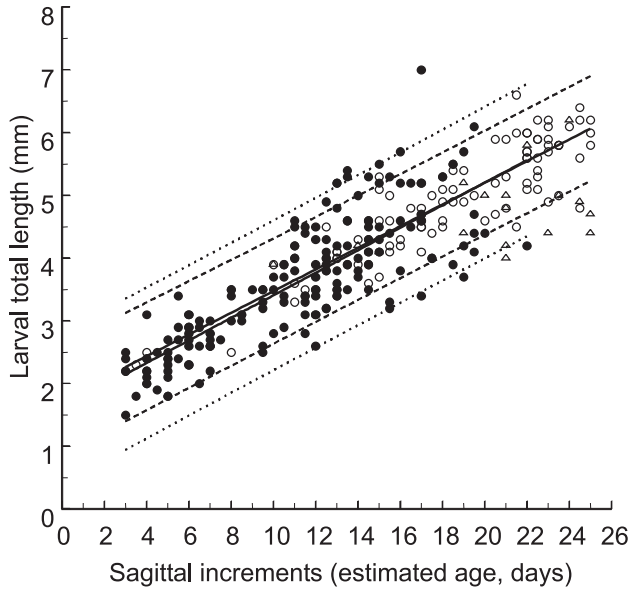
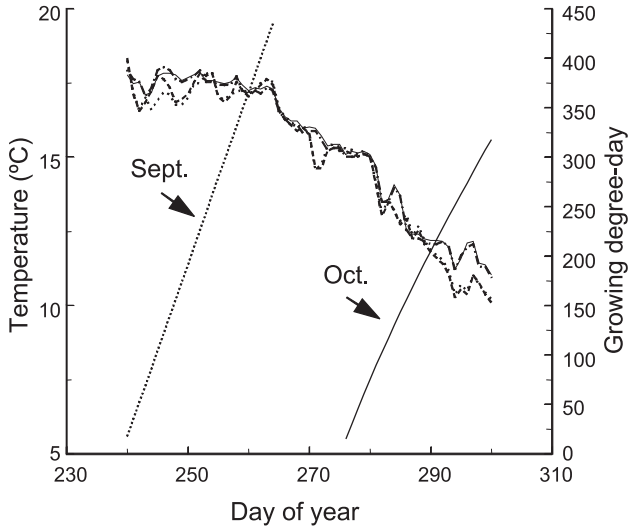


Fig. 5. Smoothed temperature time series for 28 August to 27 October 1997 (days 240–300) collected at two moorings on Western Bank at 2 m (dashed and dot-dashed lines) and 11 m (solid and dotted lines) depths. GDD trajectories for the September and October cohorts are shown as dotted and solid lines, respectively.



variation in the otolith–fish size relation may artificially create variation in AOGR that does not reflect that found in ASGR (AOGR = –23 + 1.7 × 10^3 ASGR; r^2 = 0.59). Thus, all analyses were performed using ASGR and AOGR.

The single physical variable that accounted for the most variance in ASGR in subcohort 1 was bottom depth (total depth of the water column at a given location; Table 2). Salinity averaged over the mixed layer explained the most variance in AOGR (Table 2). Multivariate analyses incorporating bottom depth, salinity, and larval silver hake concentration explained 60% of the variance in ASGR. The slope parameter for silver hake concentration was negative and had a marginal (<5%) but significant influence on the explained variance. Bottom depth, salinity, and hatch date explained 62% of the variance in AOGR.

Bottom depth and (or) salinity appear to account for a significant proportion of the variation in growth rate on Western Bank. In general, salinity and bottom depth are correlated because higher salinity water typically occurs over greater depths on the Scotian Shelf. Partial correlations between ASGR and bottom depth (salinity removed; Pearson r = 0.52, Spearman r = 0.46) and between ASGR and salinity (bottom depth removed; Pearson r = 0.25, Spearman r = 0.21) suggest that ASGR variation is better explained by bottom depth than by salinity, and bottom depth is a simple measure of geographic location on and around Western Bank. ASGR and AOGR calculated at 5-m bottom depth intervals increased by ~0.17 mm·d^{-1} and ~220 μm^2·d^{-1}, respectively, for larvae collected (over greater bottom depths) further from the crest of Western Bank (Fig. 6).

The rmMANOVA showed no difference in the trajectories of the back-calculated TL-at-age and daily growth rate series (p = 0.41 and 0.27, respectively) for the five larvae representative of each water mass on- and off-bank. However, when data for all 22 larvae were combined to define on- and off-bank TL-at-age and daily growth rate series, the slope for each series was greater for off-bank larvae than for on-bank larvae (ANCOVA, p < 0.001). Individual ANOVA at each increment using data for the 22 larvae indicated that the average back-calculated length and growth rate at each increment were not different (p > 0.005) between on- and off-bank larvae until at least 8 d had elapsed (Fig. 7). After this age, larvae collected off-bank were larger at a given age and had greater daily growth rates relative to larvae collected on-bank. In comparison, there was no difference in back-calculated TL at hatch between larvae collected on- and those collected off-bank (ANOVA, p = 0.27, N = 15).

Subcohort 2 (October)

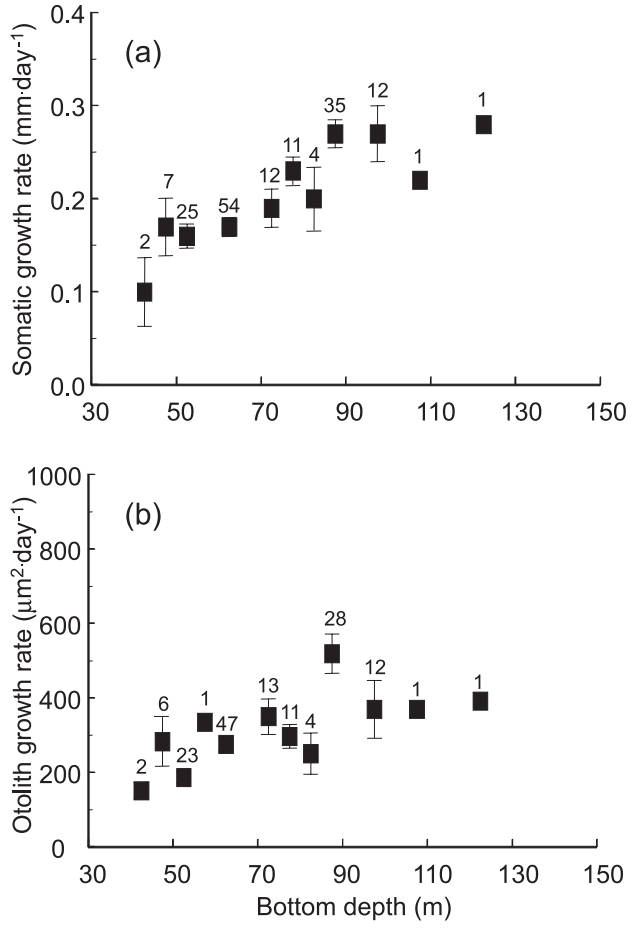
Contrary to the pattern observed in the residuals of the September cohort, the residuals of the TL-at-age relation for the October cohort showed no pattern. The relation between ASGR and AOGR calculated using eqs. 1 and 2 for larvae in subcohort 2 was weak (AOGR = –7.7 + 7.7 × 10^2 ASGR; r^2 = 0.20), perhaps reflecting the nonlinearity in the otolith–fish size relation observed for larvae collected in October. Consequently, the results differed for ASGR and AOGR. A strong relation was apparent between AOGR and larval age, hatch date, and GDD (all interrelated variables), while these relations were weak for ASGR (Table 3). Bivariate relations with all other physical and biological variables were weak at best (Table 3). As date of collection was the same for all larvae in October, it is not included in the analyses. A

Table 2. Least squares regression statistics for the relations between ASGR (N = 164) and AOGR (N = 149) and all physical and biological variables examined for silver hake larvae aged 10–20 d collected on Western Bank in September 1997.

	ASGR			AOGR		
Variable	Slope	Intercept	r^2	Slope	Intercept	r^2
Bottom depth (m)	2.8×10^{-3}	3.8×10^{-3}	0.56**	5.3	–51	0.39**
Salinity (psu)	0.13	–4.0	0.43**	3.2×10^{2}	-9.8×10^{3}	0.45**
Density ($kg \cdot m^{-3}$)	0.13	-1.3×10^{2}	0.27**	2.0×10^{2}	-2.0×10^{5}	0.13**
Silver hake concentration ($no. \cdot m^{-3}$)	-4.2×10^{-3}	0.23	0.13**	–3.8	3.5×10^{2}	0.022
Larval concentration ($no. \cdot m^{-3}$)	-3.9×10^{-3}	0.23	0.12**	–3.2	3.5×10^{2}	0.016
Zooplankton biomass ($g \cdot m^{-3}$)	–0.18	0.23	0.053*	-2.1×10^{2}	3.6×10^{2}	0.015
Hatch date (d; day of year)	1.2×10^{-3}	-9.6×10^{-2}	<0.01	–14	3.8×10^{3}	0.093**
Age (d)	-2.7×10^{-4}	0.21	<0.01	16	95	0.091**
Temperature (°C)	8.7×10^{-3}	5.3×10^{-2}	<0.01	58	-6.6×10^{2}	0.085**
GDD (°C·d)	-2.1×10^{-5}	0.21	<0.01	0.92	87	0.088**
Mixed layer depth (m)	5.9×10^{-4}	0.19	<0.01	–5.5	4.2×10^{2}	0.028*
Collection date (d; day of year)	1.6×10^{-3}	–0.22	<0.01	–4.3	1.4×10^{3}	<0.01

Note: *$p < 0.05$; **$p < 0.001$.

Fig. 6. Scattergram of average ± 2 SE (*a*) somatic and (*b*) otolith growth rates for silver hake larvae aged 10–20 d collected over 5-m bottom depth intervals on Western Bank in September 1997. Numerals above error bars indicate sample sizes.



multivariate model with GDD and depth was able to explain only 4.3% of the variance in ASGR within subcohort 2, but a multivariate model with depth and age was able to explain 38% of the variance in AOGR, with only age making a significant contribution to the explained variance.

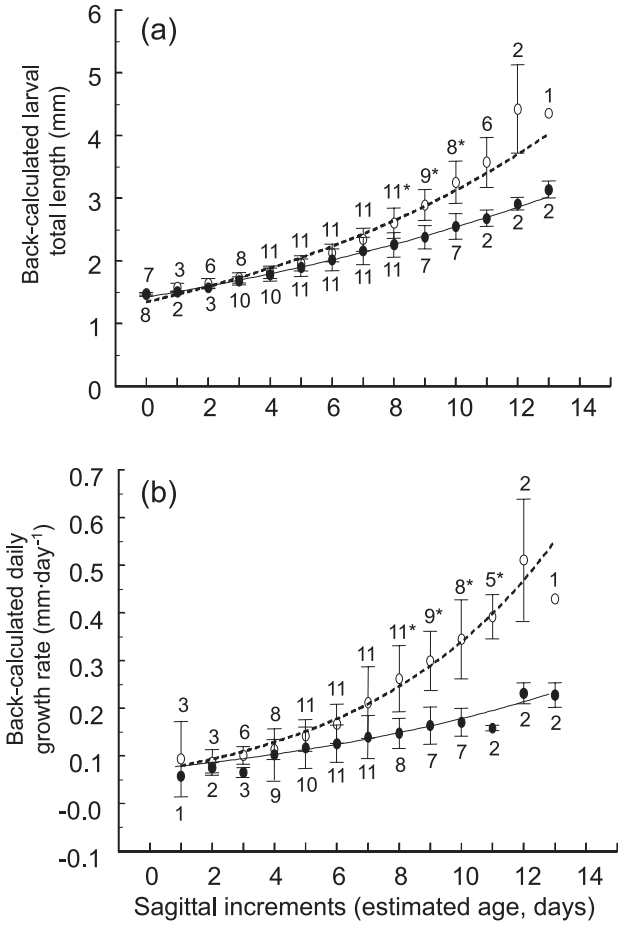
Discussion

Growth variation among monthly cohorts

The TL-at-age relations for September and October cohorts of larval silver hake on the Scotian Shelf were best described by linear least squares regression that revealed cohort-specific growth rates of 0.17 and 0.18 $mm \cdot d^{-1}$, respectively. These are the first estimates of TL-at-age relations for silver hake larvae in the northwest Atlantic that we know of. The rates are similar to that of 0.16 $mm \cdot d^{-1}$ reported for Pacific hake (*M. productus*) larvae aged at <20 d (Bailey 1982) and are within the range of 0.135–0.279 $mm \cdot d^{-1}$ reported by Cass-Calay (1997) for Pacific hake larvae collected from environments with varying prey concentrations.

We did not expect virtually identical TL-at-age relations between September and October given that the GDD estimates for these cohorts differed by ~117°C·d (analogous to an average daily temperature difference of ~4°C) and that the zooplankton biomass estimate was about twofold greater for the October cohort than for the September cohort. We are confident of the temperature data, and our use of it, given the similarities in the time series from different depths in the surface mixed layer at different locations on Western Bank and the evidence that the larvae reside in the mixed layer (Fortier and Villeneuve 1996; C. Reiss, Department of Oceanography, Dalhousie University, Halifax, N.S., unpublished data). We are wary of our interpretations related to zooplankton biomass as an index of the larval prey field, as the collections were made with large and different mesh sizes and gear types for each cohort (333-μm-mesh BONGO for September, 243-μm-mesh BIONESS for October). However, Colton et al. (1980) found no difference in the displaced volume of plankton (positively correlated with biomass) collected with 253- and 333-μm-mesh nets at tow speeds similar to those used by us (0.5–1 $m \cdot s^{-1}$). What is most important is our inability to distinguish between growth rates in cohorts that have experienced different ther-

Fig. 7. Scattergram of average (*a*) TL and (*b*) daily growth rate series (back-calculated using surface area of each increment and the biological intercept model: Campana 1990) for silver hake larvae collected on and off Western Bank in September 1997. Relationships based on all estimates are shown by the dashed (off-bank) and solid (on-bank) lines: off-bank TL = $1.4e^{(0.084age)}$, $r^2 = 0.89$; off-bank GR = $0.066e^{(0.16age)}$, $r^2 = 0.77$; on-bank TL = $1.4e^{(0.058age)}$, $r^2 = 0.88$; and on-bank GR = $0.074e^{(0.090age)}$, $r^2 = 0.45$. Average ± 1 SD TL and daily growth rate estimates (off-bank, open circles; on-bank, solid circles) and sample sizes (off-bank, above; on-bank, below) are shown for each age. Significant differences (ANOVA, $p < 0.005$) at age between on- and off-bank larvae are indicated by an asterisk.



mal and feeding environments. Thus, neither temperature nor potential prey concentration alone can explain variation in growth between monthly cohorts, and perhaps a combination of these variables may be instructive (e.g., Rutherford et al. 1997; Gallego et al. 1999). Our initial premise that cohorts experiencing different environmental conditions will have different growth rates is invalid. Further, TL-at-age relations did not differ between larvae collected during day and night (in September 1997), and we can conclude that light-dependent gear avoidance (day–night effect) is insufficient to explain the similarity in TL-at-age among cohorts of similar age.

Strong relations were observed between otolith surface area and TL for larvae collected in September, October, and November, and the relations were different. This is consistent with others who have shown otolith–fish size relations to be dependent on temperature (Mosegaard et al. 1988) or prey concentration (Secor et al. 1989) through their influence on somatic growth rate (Secor et al. 1989). We reject the widely reported hypothesis that fast-growing larvae have smaller otoliths relative to body size than do slow-growing larvae (Secor et al. 1989), at least among monthly cohorts of silver hake larvae, as the TL-at-age relations were the same for September and October. However, we were unable to reject the same hypothesis within each monthly cohort, as a significant ($p < 0.002$) positive relations was observed between the residuals of the TL-at-age relation and the residuals of the otolith–fish size relations. Thus, the explanation for variation in the otolith–fish size relations among monthly cohorts is not easily determined using these data, but variation in the relation within cohorts can, in part, be explained by variation in growth rate. We must conclude that the relation between otolith and fish size in silver hake is not robust for larvae that have experienced a variety of environmental conditions. Otolith growth trajectories should, therefore, not be compared directly for larvae in different cohorts, and cohort-specific otolith–fish size models should be developed.

Our observation that TL-at-age was similar for cohorts experiencing different environments, however surprising, is not unique. Yoklavich and Bailey (1990) found no differences in growth rates of larvae collected in different years despite an average temperature difference of ~2°C. Furthermore, no relation was observed between growth rate and temperature in Pacific hake for temperatures between 10.5 and 12.4°C (Cass-Calay 1997). We hypothesize that the similarities in growth rate among cohorts may be explained by (1) variations in temperature and zooplankton biomass (potential prey) that were insufficient to produce a measurable difference in growth rate, (2) synergistic effects of temperature and zooplankton biomass on growth, and (3) enhanced prey requirements for larvae with increased metabolic rates related to higher water temperatures (Anderson 1988). Hypotheisis 1 is an unlikely explanation given the large ranges in temperature and prey levels experienced by the September and October cohorts. The other two hypotheses are not as easily dismissed. Larvae in the September cohort had a higher GDD history and nearly half the zooplankton biomass relative to those in the October cohort. Temperature and prey concentration may therefore have acted in concert to result in similar growth rates (hypothesis 2), or the lower potential prey levels in September may have been insufficient to meet the increased metabolic demand incurred by the higher GDD (hypothesis 3). It will be logistically difficult to distinguish between hypotheses 2 and 3 in field studies. However, the hypothesis that temperature and prey levels interact to determine TL-at-age relations in monthly cohorts of silver hake larvae can and should be tested using independent data derived from larval cohorts that have experienced different temperature and prey field histories.

The similarity in slopes of the TL-at-age relations for the September and October cohorts, despite different environmental conditions, indicates that aggregate estimates of larval growth at the monthly scale may be of limited value in predicting growth rate using environmental measures and

Table 3. Least squares regression statistics for the relations between ASGR and AOGR and all physical and biological variables examined for silver hake larvae aged 10–20 d (N = 53) collected on Western Bank in October 1997.

	ASGR			AOGR		
Variable	Slope	Intercept	r^2	Slope	Intercept	r^2
Bottom depth (m)	-2.3×10^{-4}	0.19	0.040	0.19	1.2×10^{2}	<0.01
Salinity (psu)	2.8×10^{-2}	–0.70	0.045	16	-3.6×10^{2}	<0.01
Density ($kg \cdot m^{-3}$)	2.8×10^{-2}	–29	0.05	16	-1.6×10^{4}	<0.01
Hake concentration ($no. \cdot m^{-3}$)	2.9×10^{-2}	0.17	0.022	–48	1.4×10^{2}	0.021
Larval concentration ($no. \cdot m^{-3}$)	2.9×10^{-2}	0.17	0.023	–46	1.4×10^{2}	0.020
Zooplankton biomass ($g \cdot m^{-3}$)	1.2×10^{-2}	0.17	<0.01	–57	1.5×10^{2}	0.031
Hatch date (d; day of year)	6.3×10^{-4}	-1.4×10^{-3}	<0.01	–10	3.1×10^{3}	0.38**
Age (d)	-6.3×10^{-4}	0.19	<0.01	10	–34	0.38**
Temperature (°C)	-1.1×10^{-2}	0.30	0.023	–17	3.1×10^{2}	0.018
GDD (°C·d)	-5.1×10^{-5}	0.19	<0.01	0.80	–24	0.38**
Mixed layer depth (m)	5.6×10^{-4}	0.16	<0.01	–3.1	2.5×10^{2}	0.032

Note: *$p < 0.05$; **$p < 0.001$.

may not prove useful in the prediction of survival based on growth. Our suggestion is consistent with the idea that predicting growth, and ultimately survival, using environmental variables requires analysis at finer scales within cohorts and among individuals (Rice et al. 1993; Chambers and Miller 1995; Rutherford and Houde 1995). The results reported here benefit from a species and system that permit the finer scales of growth variability to be examined.

Growth variation within subcohorts

The residuals of the TL-at-age relations revealed growth to be a systematic function of geographic location within the September but not within the October cohort. This demonstrates the value of examining growth variation among months and cohorts, as conclusions based on results from one cannot be assumed to apply to another. The mostly positive residuals and higher ASGR and AOGR for larvae collected in deeper water off the crest of Western Bank during September indicate that larvae swept from the bank incur a growth advantage over larvae retained on the bank. Such an interpretation is consistent with Buckley and Lough (1987) and Frank and McRuer (1989) who observed that haddock (*Melanogrammus aeglefinus*) larvae in the shallow, mixed conditions on Georges Bank and Browns Bank, respectively, were in worse condition than larvae collected in deeper, stratified waters. Shackell et al. (1999) provided evidence that haddock advected from the Browns Bank region as larvae displayed greater size at age as juveniles than those presumed to have been retained as larvae on the bank. However, those same authors also provided evidence that the juveniles on Browns Bank had a lower overall mortality than those found elsewhere. Their findings are inconsistent with the hypothesis that slow growth is coupled with high mortality.

The variation in growth rates observed on- and off-bank indicates that growth is not homogeneous in the Western Bank region during late September at scales of ~15 km or less. This has serious implications for sampling and the estimation of population or cohort growth rates as they could be easily biased (high or low) depending on the water masses that represent the majority of the sampling. If growth estimates are biased, then survival estimates based on growth rate will be likewise.

We do not know what is directly responsible for the growth advantage observed for off-bank larvae. However, in this region the shelf break current is bathymetrically steered (Loder et al. 1997; Reiss et al. 2000) around Western Bank in an anticyclonic manner and larvae swept off-bank become entrained in a different water mass relative to those remaining on-bank. Possible explanations for the higher growth rates off-bank include (*i*) size-selective predation on- or off-bank, (*ii*) food limitation on-bank where larval concentrations are initially high, and (*iii*) a common origin for on- and off-bank larvae and enhanced growth for larvae transported off-bank. The similar variance in growth rates on- and off-bank and the negative relation between ASGR and larval concentration (silver hake or all species) are inconsistent with size-selective predation (hypothesis 1). The negative relation between ASGR and silver hake concentration does suggest that larvae on-bank may be food limited at high larval concentrations. No relation was observed between somatic growth rate and zooplankton biomass among locations on- and off-bank, and the results are therefore inconsistent with food limitation (hypothesis 2) and inferences that larval nutrition is inadequate off-bank (McLaren and Avedaño 1995). The analysis of individual growth trajectories for larvae collected on and off Western Bank indicates that the back-calculated TL-at-hatch was similar for all larvae and the average back-calculated TL-at-age and daily growth rate of larvae from the two water masses were similar until ~8 d posthatch. After this the larvae collected off-bank had a greater TL-at-age and a greater daily growth rate. Using the scaling arguments of Loder et al. (1988), the time scale for the along-bank drift was estimated as ~10 d using the average current speed (0.07 $m \cdot s^{-1}$, derived from the in situ current meters) and the along-bank length scale (60 km). This is of the same order as the observed divergence in growth rates of larvae on- and off-bank at 8 d posthatch. Thus, the variation in growth rates is most easily explained by the larvae having a common origin near the crest of Western Bank (consistent with O'Boyle et al. 1984) and those transported off-bank incur a growth advantage in the new water mass (hypothesis 3). We therefore hypothesize that growth variability within cohorts is determined by larval transport and the resulting water mass associations. Thus, the analyses of growth varia-

tion in relation to physical oceanographic conditions will be required for predictions of larval growth variation in space.

The differences in average growth series on- and off-bank are not statistically supported by the rmMANOVA performed with five larvae from each water mass. This is related to the small sample size and the short time series (less than increment 10) that are a function of electing to measure the more conservative and less biased surface area of each otolith increment as opposed to increment widths along a single axis. The rmMANOVA results should thus be interpreted with caution, as the individual series extend over the first 10 d posthatch and the separation in growth trajectories determined at the population level only becomes apparent at 8 d. Furthermore, there is some uncertainty about the accuracy of daily otolith measurements for predicting daily somatic growth within individual larvae due to variation in the otolith–fish size relationships. However, in this study the somatic growth histories are back-calculated for relative comparisons among larvae in different water masses and the actual back-calculated sizes and growth rates are of little concern. We are confident that our results represent the relative differences in the daily growth series for larvae collected on- and off-bank.

In contrast with that observed in September, no clear relation was observed between growth rate and water mass structure, or geographic location, or any of the biological variables measured in October, perhaps due to the spatially constrained sample collections in October. We resampled the September collections in a manner that approximated the spatial distribution of the October collections to test this hypothesis. The results indicated that the proportion of the variance in growth rate explained by environmental variables (bottom depth, salinity, density, larval concentration, silver hake concentration, and zooplankton biomass) decreased when the September collections were spatially constrained. Therefore, we cannot reject the hypothesis that the lack of pattern in the October data is in part due to the spatially constrained samples collected during this period.

Based on hypotheses that suggest that larger or faster growing larvae have a survival advantage over smaller, slower growing larvae (Miller et al. 1988; Rice et al. 1993; Meekan and Fortier 1996), the results of this study suggest that survival should be greater for silver hake larvae that are removed from the crest of Western Bank early in development. However, as pointed out above, Shackell et al. (1999) gave evidence that this may not always be so. Clearly, examining larval growth and survival in relation to transport processes and at the scale of water masses within monthly cohorts may provide clarity and prove useful for predicting larval survival.

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