# An Age- and Temperature-Mediated Growth Model for Cod (*Gadus morhua*) and Haddock (*Melanogrammus aeglefinus*) Larvae in the Gulf of Maine[1]

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While field studies of larval fish growth require an easily parameterized growth model, simple relationships between size and age are seldom applicable to other populations and/or environments. The model presented here attempts to bridge the gap between simple age–length regressions and more sophisticated experiment-based models by incorporating a temperature term as a function of absolute growth rate. Growth is assumed to be logistic, with temperature influencing growth rate parabolically on a daily basis. The integrated form of the model provides an estimate of length-at-age of the larva. When fitted to a variety of independent cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) data sets collected in the Gulf of Maine, the model performed with minimal bias despite the absence of a food availability term. Larval age data were generated through validated otolith microstructure examinations, although the resolution limits of light microscopy introduced a small degree of bias (2–3 d) into the estimates. The daily temperature record was generated from a sinusoidal model using monthly mean temperatures. Since otolith microstructure examination and remote sensing of temperature are established techniques, this model may prove useful in other larval studies.

Bien que les études de croissance des larves de poisson réalisées sur le terrain doivent pouvoir se fonder sur un modèle de croissance facilement paramétrisé, il est rarement possible d'appliquer des rapports simples entre la taille et l'âge à d'autres populations et/ou d'autres milieux. Le modèle présenté ici tente de combler le vide entre les régressions simples âge-longueur et les modèles plus sophistiqués, élaborés à partir d'expériences, en incorporant un terme de température, qui est fonction de la vitesse de croissance absolue. La température joue un rôle sur la vitesse de croissance de façon parabolique sur une base quotidienne. La forme intégrée du modèle fournit une estimation de la longueur en fonction d'un âge donné de la larve. Le modèle, appliqué à diverses séries de données indépendantes sur la morue (*Gadus morhua*) et l'aiglefin (*Melangrammus aeglefinus*) prélevés dans le golfe du Maine, a présenté un biais minimum malgré l'absence d'un terme de disponibilité de nourriture. Les données sur l'âge des larves ont été produites par des examens validés des microstructures des otolithes, bien que les limites de résolution de la microscopie optique aient introduit un petit biais (2–3 d) dans les estimations. Une liste des températures journalières a été produite à partir d'un modèle sinusoïdal fondé sur les températures moyennes mensuelles. Étant donné que l'examen des microstructures d'otolithes et la télédétection des températures sont des techniques reconnues, ce modèle pourrait servir à d'autres études sur les larves.

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Predictive growth models for larval gadids span the range from simple linear regression of length on age (Anderson 1982; Yin and Blaxter 1986) to sophisticated environment-mediated foraging calculations (Beyer and Laurence 1981; Ellertsen et al. 1981). The degree of sophistication and predictive power in these studies is often inversely related to the level of the experimenter's control; complex models are not easily parameterized in field situations, nor are they necessarily intended to be. Yet realistic growth models of wild fish larvae often form the basis for models of higher-order processes such as recruitment and survival (e.g. Jones 1973; Leak and Houde 1987). The realities of monitoring the growth and environment of marine larvae in situ have constrained previous workers to the fitting of imprecise and/or point specific length-at-age curves. For this reason, we see the need for an easily-parameterized growth model of intermediate complexity, with powers of prediction for wild larvae, and the flexibility necessary for application to a broad range of environmental conditions and/or populations. Such a model is presented here in application to larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in the Gulf of Maine.

Current models of the growth of larval cod and haddock are largely based upon the results of laboratory (Laurence 1974, 1978; Beyer and Laurence 1981; Laurence et al. 1981; Gamble and Houde 1984; Yin and Blaxter 1986) and enclosure (Ellertsen et al. 1981; Gamble and Houde 1984; Kvenseth 1984) studies. Growth data were modelled primarily as a function of age, with prey availability, temperature, and other variables incor-

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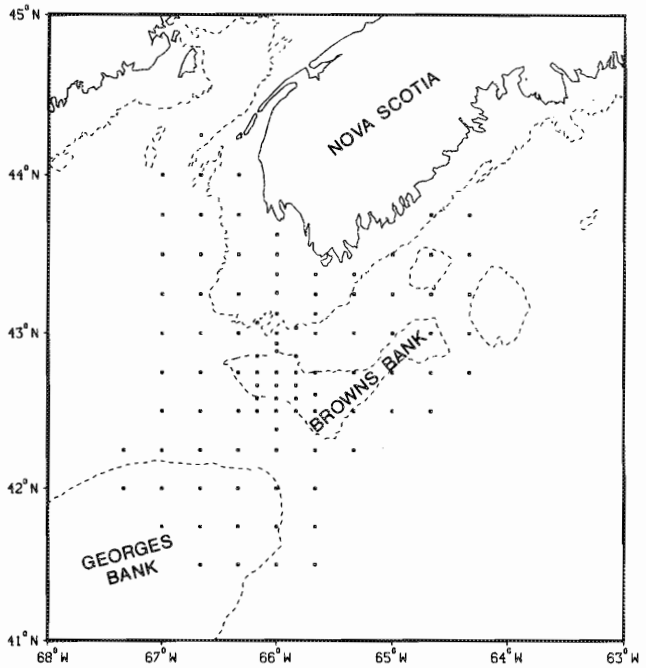


FIG. 1. The location of sampling stations relevant to this study during the ichthyoplankton survey of southwest Nova Scotia in 1984 and 1985. Coverage of the survey grid varied slightly among cruises (Table 1).

TABLE 1. Summary of cruises represented in this study.

| Year | Cruise | Date | Number of stations sampled | Number of larvae examined: Cod | Number of larvae examined: Haddock |
|---|---|---|---|---|---|
| 1984 | H114 | March 12–30 | 54 | 7 | 67 |
| | H116 | April 16–27 | 59 | 100 | — |
| 1985 | H130 | Feb. 4–22 | 93 | 15 | — |
| | H132 | March 11–29 | 49 | 42 | 7 |
| | H133 | April 2–17 | 90 | 202 | 40 |
| | H135 | May 6–16 | 57 | 95 | 136 |
| | H137 | June 3–14 | 59 | 35 | 372 |

porated as accessory variables into the more complex models. While age data are intrinsic to controlled experiments, they have (until recently) been difficult to obtain in field studies. Therefore, earlier field studies of larval cod and haddock growth necessarily adopted length-frequency analysis as a proxy for age, despite the confounding effects of immigration/emigration, size-selective mortality and an extended spawning period (Graham 1933; Saville 1956; Anderson 1982). All of these effects can skew a length-frequency mode, thus making it difficult or impossible to track a larval cohort and/or assess its rate of growth. With the advent of otolith microstructure examination as a more precise age determination tool (Pannella 1971; Brothers et al. 1976; reviewed by Campana and Neilson 1985), direct age measurements of field-collected larvae became possible. Such measurements have been used to advantage in other field studies of larval gadoids (Nishimura and Yamada 1984; Walline 1985; Kendall et al. 1987), as well as in the only other field study of larval gadid age structure in the Gulf of Maine (Bolz and Lough 1983). It is also the approach adopted here.

In this paper, we wish to reassess the results of Bolz and Lough (1983) in light of recent findings concerning apparent bias in otolith microstructure studies (Geffen 1982; Campana et al. 1987), as well as extend the scope of their study beyond that of a point estimate. Accordingly, we shall evaluate the spatio-temporal variation in larval growth rate over a broad region and sequence of surveys, encompassing the waters in and around Browns and Georges Bank in 1984 and 1985. A third objective is to develop a generalized growth model to fit these data, with the view towards making it broadly applicable to other areas and times. Finally, we use the model to test competing hypotheses concerning the relative growth of cod and haddock larvae under a variety of environmental regimes (Laurence 1978; Laurence et al. 1981).

## Materials and Methods

Cod and haddock larvae were collected in seven different cruises over a fixed survey grid as part of the Fisheries Ecology Program ichthyoplankton survey. The survey encompassed 97 stations to the south, east, and west of Nova Scotia, down to and including portions of Georges Bank (Fig. 1). Surveys represented in this study were conducted in March and April of 1984 and monthly between January and June of 1985, although weather restricted grid coverage on some cruises (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. Full sampling details and cruise-by-cruise station locations are documented elsewhere (P.C. Hurley and S.E. Campana, unpubl. data).

Upon collection, unsorted samples were preserved in 5% formalin: saltwater made basic to a pH of 8.0–9.0 with sodium carbonate; the latter retarded acidic degradation of the otoliths until the samples could be preserved in 95% ethanol. Samples were transferred to 95% ethanol for storage within 3 wk of collection. Prior to otolith removal, larvae were 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 according to standard techniques (Campana and Neilson 1985). All otoliths with diameters exceeding 40 μm were polished with lapping film prior to microscopic examination. Otoliths showing evidence of formalin degradation (brown discolouration, pitting) were not considered further. Degraded otoliths constituted approximately 20% of the total number (primarily in Cruise H135), although the proportion degraded 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 system 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 resolution loss during increment counts were generated through the increment width estimation procedure described in Campana et al. (1987). Briefly, this involved the fitting of a logistic curve to the increment count data associated with each otolith growth diameter (OGD = otolith diameter — hatch check diameter), and then using the fitted model

TABLE 2. Sinusoidal model used to generate a daily sea surface temperature record from mean monthly temperatures. Separate models were developed for Browns and Georges banks in each of 1984 and 1985. DOY = day of year.

$$\text{Model: Temp(°C)} = \left(a\text{Sin}\left(\left(\frac{2\pi}{365}(\text{DOY} + b)\right)\right) + c\right)$$

| | | Parameter estimate | | | | Estimated temperature | | |
|---|---|---|---|---|---|---|---|---|
| Region | Year | $a$ | $b$ | $c$ | $R^2$ | Jan. 1 | March 1 | June 1 |
| Browns | 1984 | 5.350 | −158.5 | 8.417 | 0.98 | 6.2 | 3.1 | 7.7 |
| | 1985 | 5.301 | −161.1 | 8.355 | 0.99 | 6.4 | 3.1 | 7.4 |
| Georges | 1984 | 5.088 | −156.9 | 9.616 | 0.99 | 7.4 | 4.6 | 9.1 |
| | 1985 | 5.187 | −159.5 | 9.290 | 0.97 | 7.2 | 4.2 | 8.5 |

TABLE 3. Increment width at Age 1 day in the otoliths of cod and haddock larvae collected on several cruises. The 1984 larvae were collected on Georges Bank while the 1985 samples were from the vicinity of Browns Bank. Widths were estimated for each otolith type from the logistic model relating increment count to otolith growth diameter in each larva (see text for details). * = Poor fit of model (pattern in residuals), rendering width estimation inappropriate.

| | Increment width (μm) at Age 1 day | | | |
|---|---|---|---|---|
| | Cod | | Haddock | |
| Cruise date | Lapillus | Sagitta | Lapillus | Sagitta |
| 1984; March 12–30 | 0.33 | 0.40 | 0.54 | 0.33 |
| 1985; March 11–29 | 0.42 | 0.42 | — | * |
| April 2–17 | 0.37 | 0.43 | 0.45 | * |
| May 6–16 | 0.39 | 0.37 | 0.44 | * |
| June 3–14 | 0.25 | 0.19 | 0.53 | 0.63 |

to estimate increment width in the first few days posthatch. Specifically, OGD was related to increment count ($C$) in the logistic equation

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

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

To determine the frequency of increment formation in newly-hatched cod larvae, samples of known age larvae were obtained incidentally from two separate experiments conducted by J. D. Neilson and K. G. Waiwood of the St. Andrews Biological Station, N.B. In both experiments, larvae were reared from the egg stage under a diel light cycle (12 h light:12 h dark) and ambient temperatures of 5–6°C (Exp. 1: 29 April–13 May 1983, $N$ = 42; Exp. 2: February 7–March 4, 1984, $N$ = 8). Larvae were fed twice daily with rotifers. Sampled larvae were preserved in 95% ethanol prior to otolith removal. Microstructural examinations were made as described above without knowledge of true larval age or sampling frequency.

Vertical temperature profiles were made at each cruise station. However, retrospective analysis of larval growth required a daily sequence of water temperatures. Daily temperature series for 1984 and 1985 were generated from mean monthly temperatures (NOAA 1984, 1985) in two areas: Browns and Georges banks. Sinusoidal least-squares regressions were fit to the monthly data, with the resulting equations used to predict the daily sea surface temperature (SST) record for each region (Table 2). The predicted temperature values were consistent with those actually observed during each cruise.

TABLE 4. Results of the first experiment reporting the frequency of increment formation in newly hatched cod larvae.

Experiment 1.

Model: Increment count = $a + b$ (Age)
Range of ages = 0–14
$N$ = 42
$P < 0.001$
$R^2$ = 0.80

| Parameters: | Estimate | SE | Significance |
|---|---|---|---|
| Intercept | −0.45 | 0.63 | 0.48 |
| Slope | 0.89 | 0.069 | <0.001 |

TABLE 5. Results of the second experiment reporting the frequency of increment formation in newly hatched cod larvae.

| Sample | $N$ | Age (d) | Mean count |
|---|---|---|---|
| 1 | 3 | 14 | 17 |
| 2 | 2 | 16 | 15 |
| 3 | 2 | 4 | 7 |
| 4 | 1 | 26 | 16 |

Parameters for larval and otolith growth models were generated 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). 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 set at 0.05 for all tests.

## Results and Discussion

### Estimation of Age, Resolution Loss, and Length

The otolith microstructure of the cod and haddock larvae was largely unambiguous in its interpretation. Intra-larval increment counts were highly correlated both within an otolith type and between lapillae and sagittae (slope = 1.0 ± 0.05; $R^2 > 0.95$) in both species. However, the intercept term for the regression of sagittal counts on lapillar counts was highly significant, and indicated that the latter exceeded the former by an average of 2.6 and 1.6 for cod and haddock, respectively. Given the smaller size of the sagittae at hatch and the very narrow (<0.5 μm) increments encircling the nucleus (Bolz and Lough 1983; 1989), Campana resolution limitations associated with the use of light microscopy were suspected to be the source of the inter-otolith discrepancy (Campana et al. 1987). The significance of this

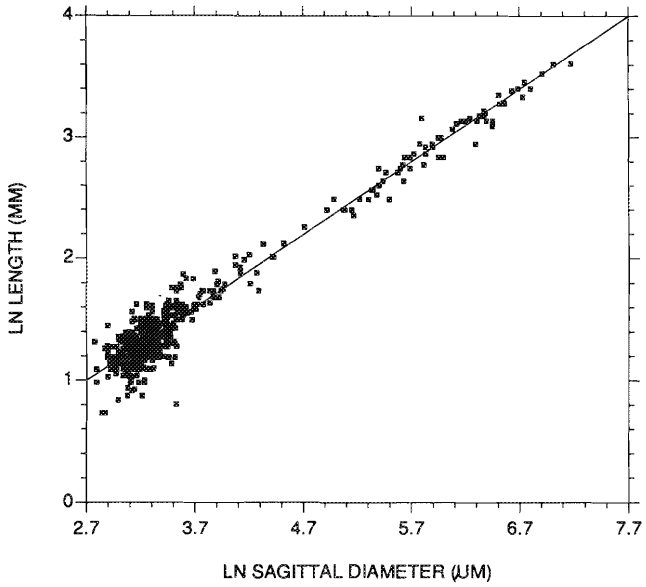


FIG. 2. Regression of cod larval length on maximum sagittal diameter, with both axes ln transformed. Since the unaggregated relationships were not significantly different among themselves, cod data were aggregated across years, cruises, and regions.

suspicion is that increment counts would underestimate the number actually present if increments were too narrow to resolve as individual units. In the case of larval herring (*Clupea harengus*), resolution-limited increment counts resulted in serious underestimates of age (15–20 d) (Campana et al. 1987). The existence of a significant, within-larva correlation ($P < 0.01$) between the intersagittal differences in growth radius and increment count, confirmed the presence of resolution-limited increment visibility in all large samples of cod and haddock larvae. Since a significant relationship was also observed among the lapilli, estimates of the magnitude of the resolution loss were deemed necessary.

Increment widths at age from each of the cruise collections were compared both with the functional resolution limit of our microscope system, and among themselves, in order to assess the relative magnitude of the potential count bias. Increment widths at day 1 were close to the resolution limit of our system for sagittae and lapilli in both cod and haddock in all cruises (Table 3). However, the increment widths increased rapidly with age, suggesting that unresolved increments, if they existed, were associated only with the youngest larvae. Haddock increment widths at day 1 tended to be larger than those of cod.

The validity of using increment counts to estimate the age of cod and haddock larvae was assessed in the first validation experiment. Increment counts were highly correlated with age in both sagittae and lapilli (Table 4). In addition, a daily frequency of increment formation in the lapilli was indicated by a regression of increment count on age not significantly different from 1.0. However, the regression slope was significantly less than 1.0 for the sagittae, and indeed, increment counts tended to underestimate age in both otolith types. Since the age-increment discrepancy stabilized in both otolith types before day 10 (asymptotic discrepancy = 2–3 and 5–6 for lapilli and sagittae, respectively), resolution limitations induced by light microscopy were again suspected. The generally good fit between the ages and increment counts in Exp. 2 (Table 5) was also consistent with resolution-limited visibility, since the one poorly-predicted age was associated with a very slow-growing larva.

In a procedure analogous to that applied to the wild larvae, increment width at day 1 was estimated for the known age larvae in Exp. 1. The resultant values (lapilli, 0.31 µm; sagittae, 0.36 µm) fell within the lower range observed among the wild larvae (Table 3), and were probably not different from our functional resolution limit. Accordingly, we have assumed that increment counts in the wild larvae underestimated larval age to an extent similar to that observed in the laboratory. Given hatch check formation in larval cod on day 1 (Bergstad 1984; Dale 1984), and the close similarity of haddock otolith microstructure to that of cod (Bolz and Lough 1983; Campana 1989), our daily increment counts appear to have underestimated age in these two species by 1–2 and 4–5 d for the lapilli and sagittae, respectively; this level of bias was considered both acceptable and unavoidable. Therefore, estimates of larval age were calculated by adding one (corresponding to the age at hatch check formation) to the mean count in the lapilli (or sagittae, if larger).

Variability is introduced into measurements of larval length through factors such as net handling time, preservation schedule, etc. (Radtke and Waiwood 1980; Fowler and Smith 1983), all of which may deform the soft tissues of a larva and vary in magnitude from sample to sample. This variability was reduced through use of sagitta length as a correlate of total length in cod larvae. The rigid sagittae can be precisely measured, are unaffected by factors other than those that cause dissolution, and were linearly related to larval length after ln-ln transformation (Fig. 2), as in

$$\ln L = 0.5996 \cdot \ln Sag - 0.6199 \quad N = 507; R^2 = 0.95,$$

where $L$ = total length of the larvae (millimetres) and $Sag$ = maximum sagittal length (micrometres). Tests for a variety of factor effects indicated that the assumption of a common slope and intercept was justified across regions, cruises and years (ANCOVA, $P > 0.1$) (S. E. Campana 1989). Accordingly, sagittal measurements were used to more precisely estimate cod larval length in the growth models that follow. While at first glance similar relationships could have been generated for haddock larvae, and for lapilli of both species, consistent (albeit minor) patterns in the residuals among cruises suggested that they not be applied (Campana 1989).

## Growth as a Function of Age

On a cruise-by-cruise basis, cod (Fig. 3) and haddock (Fig. 4) larval length was successfully modelled as a function of age, using the exponential equation

$$L = \exp(a + b \cdot \text{age}),$$

where $a$ and $b$ are regression parameters. All model fits were unbiased and highly correlated, with the correlation coefficients for cod generally exceeding those for haddock (Table 6). While specific growth rates for cod and haddock did not differ significantly within a cruise and region, such an analysis is of little value without reference to the range of ages present in the data; this fact is also at least partially responsible for the differing magnitudes of the correlation coefficients between species.

Attempts to fit the exponential model of larval growth to data aggregated on a regional (Browns versus Georges banks) and/or yearly basis were unsuccessful; the residuals formed a clear pattern across ages and cruises. While use of the log-transformed logistic model

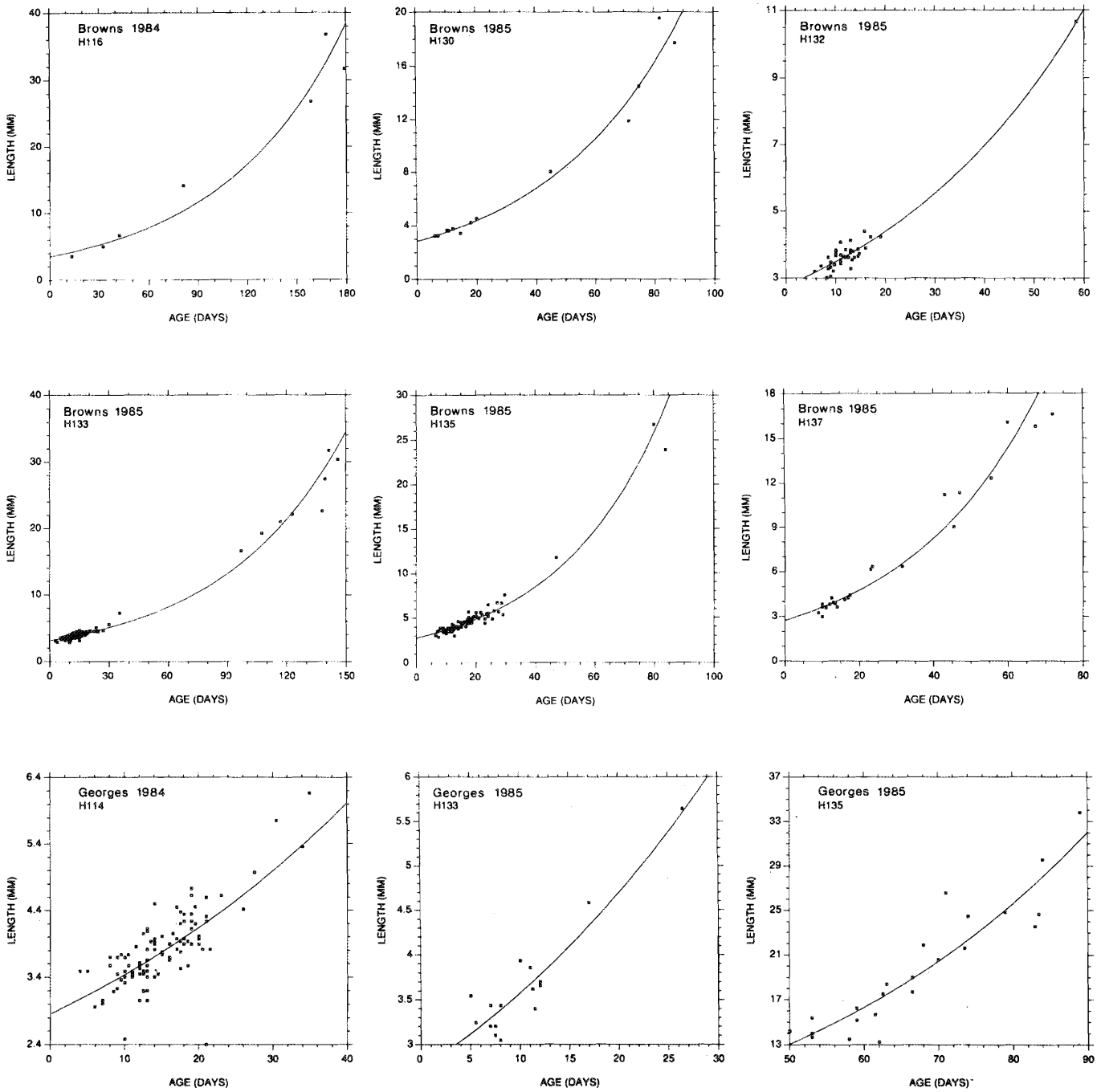


FIG. 3. Exponential growth models for cod larvae collected on each of seven cruises on Browns and Georges banks in 1984 and 1985.

$$\text{Ln } L = \text{Ln } (a + b \div (1 + \exp(-c(\text{age} - d)))),$$

where $a$, $b$, $c$, and $d$ are model parameters, improved the overall model fit, strong trends in the residuals persisted when examined on a cruise-by-cruise basis.

## Development of an Age- and Temperature-Mediated Growth Model

Given the inadequacy of the simple age-based models in application to the aggregated regional data sets, more complex models were developed which incorporated temperature as an accessory variable. Temperature is widely recognized as a significant modifier of the growth rate of fishes. Justification for the inclusion of temperature in this study was based upon laboratory demonstrations of temperature-mediated growth rates in gadid larvae (Laurence 1978; Buckley 1984). Further justification was derived from this study in the form of a significant relationship between mean SST during each cruise and the calculated specific growth rate of cod larvae less than 30-d old in each cruise collection ($P = 0.02$, $R^2 = 0.64$). While the relationship was not significant for haddock larvae, the haddock data exhibited a similar trend. Established principles concerning temperature effects on growth processes (Brett 1979; Ricker 1979) suggested the need for a logistic growth model where temperature influenced absolute growth rate in a parabolic fashion. However, in keeping with the principle of parsimony, model development began with the simplest possible formulation, progressing to more complex designs only if the statistical criteria for the simpler model were not met.

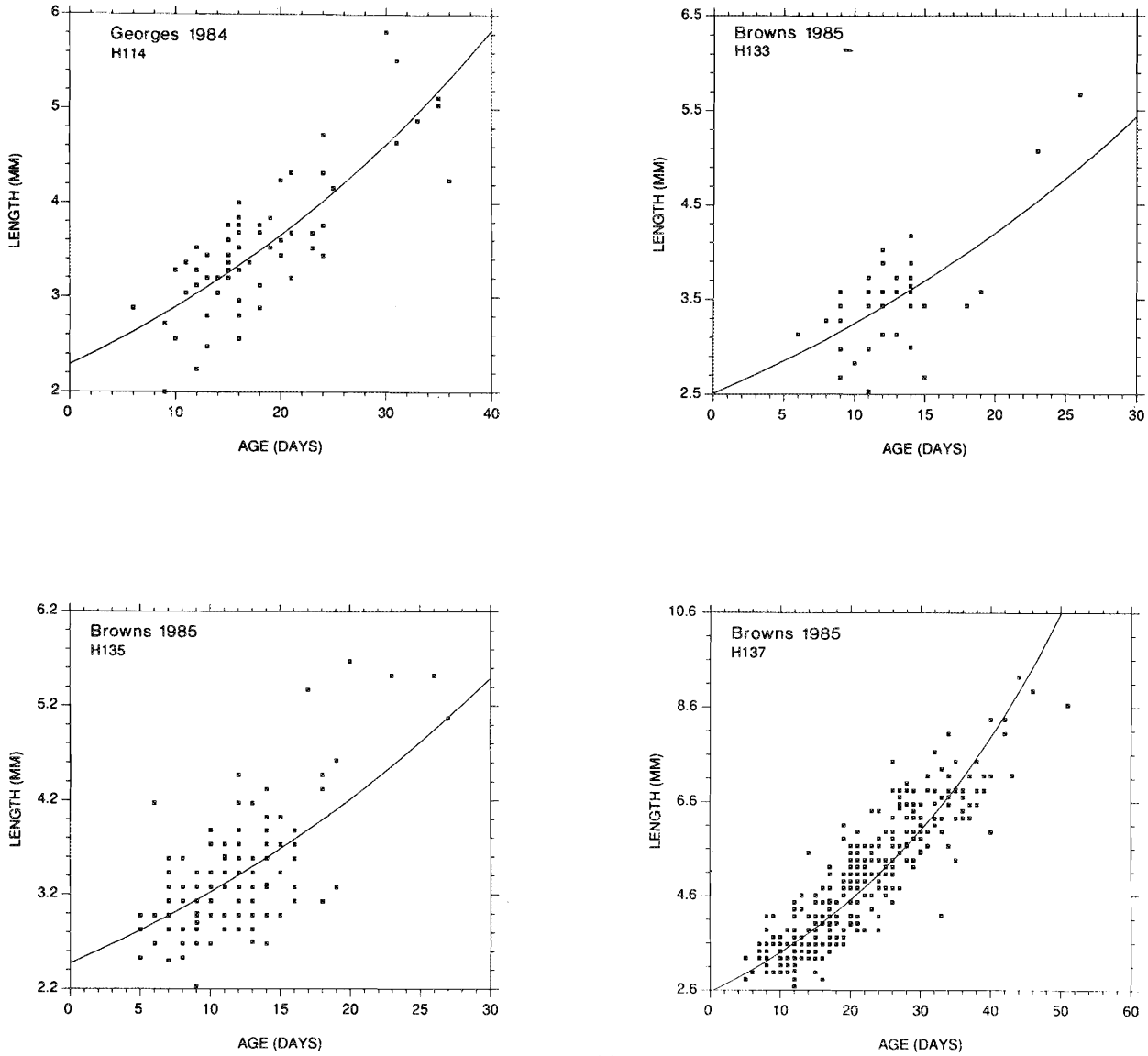


FIG. 4. Exponential growth models for haddock larvae collected on each of four cruises on Browns and Georges banks in 1984 and 1985. Model statistics are presented in Table 6.

TABLE 6. Parameters and diagnostics of an exponential growth model $L = \exp(a + b \cdot \text{age})$ fitted to cod and haddock larvae (Fig. 3 and 4) on a cruise-by-cruise and regional basis. All models were highly significant. Specific growth rates (percent·d$^{-1}$) for each cruise, region, and species are also presented.

| | | | | Intercept ($a$) | | Slope ($b$) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | Region | Year | Cruise date | Estimate | SE | Estimate | SE | $N$ | $R^2$ | Specific growth rate |
| Cod | Browns | 1984 | April 16–17 | 1.24 | 0.13 | 0.0133 | 0.0011 | 7 | 0.97 | 1.33 |
| | | 1985 | Feb. 4–22 | 1.04 | 0.03 | 0.0217 | 0.0001 | 14 | 0.99 | 2.18 |
| | | | March 11–29 | 1.02 | 0.02 | 0.0230 | 0.0012 | 39 | 0.91 | 2.30 |
| | | | April 2–17 | 1.13 | 0.01 | 0.0161 | 0.0002 | 184 | 0.97 | 1.61 |
| | | | May 6–16 | 1.02 | 0.02 | 0.0278 | 0.0009 | 69 | 0.94 | 2.78 |
| | | | June 3–14 | 1.01 | 0.04 | 0.0275 | 0.0011 | 24 | 0.96 | 2.75 |
| | Georges | 1984 | March 12–30 | 1.04 | 0.03 | 0.0186 | 0.0018 | 100 | 0.52 | 1.86 |
| | | 1985 | April 2–17 | 1.00 | 0.04 | 0.0272 | 0.0033 | 16 | 0.83 | 2.72 |
| | | | May 6–16 | 1.45 | 0.14 | 0.0225 | 0.0020 | 24 | 0.85 | 2.25 |
| Haddock | Browns | 1984 | March 12–30 | 0.828 | 0.044 | 0.0234 | 0.0023 | 67 | 0.61 | 2.34 |
| | | 1985 | April 2–17 | 0.920 | 0.070 | 0.0258 | 0.0053 | 38 | 0.40 | 2.58 |
| | | | May 6–16 | 0.905 | 0.034 | 0.0266 | 0.0028 | 130 | 0.41 | 2.66 |
| | | | June 3–14 | 0.941 | 0.017 | 0.0284 | 0.0007 | 370 | 0.79 | 2.84 |

The heterogeneity of larval ages evident in all of the samples implies that the history of temperature exposure will have differed for most larvae. Because the growth response to temperature is seldom constant across all ages/sizes (Ricker 1979), any calculations for a daily growth–temperature interaction would have to be estimated for each individual larva. The simplest form of such an interaction is that of a linear relationship between absolute growth rate and temperature, or equivalently, the hyperbolic or degree–day relationship of salmonid egg development models (Ricker 1979). This form of interaction assumes a growth response to temperature analogous to that of metabolic rate, but is formulated to deal with the changes in absolute growth rate that often occur as a fish ages. Because it is virtually impossible to monitor the growth rate of individual wild fish on a daily basis, the model was integrated to reflect larval length-at-age upon sampling, as in

$$(1)\quad L_{age} = L_{hatch} + \int_{t=0}^{age} (\text{Absolute growth rate} \times \text{Temperature})\, dt$$

The form of the absolute growth rate term ($^{dL}/_{dt}$) depends on the model selected, but since the exponential model described earlier was applied successfully on a cruise-by-cruise basis, it was also the initial choice here. This results in:

$$(2)\quad L_{age} = L_{hatch} + \int_{t=0}^{age} (aGe^{Gt} \cdot T_t)\, dt$$

and the discrete approximation:

$$(3)\quad L_{age} = L_{hatch} + \sum_{t=0}^{age} (aGe^{Gt} \cdot T_t),$$

where $L_{hatch}$, $a$, and $G$ are model parameters, $G$ is the instantaneous (or specific) growth rate, $T_t$ is temperature on the appropriate Julian day, and $t$ is time (days). The term $aGe^{Gt}$ is the derivative of the exponential growth model, or equivalently, the absolute growth rate at age $t$. Using the daily temperature record (Table 2) and the age of each larva, model (3) was fit to the data from Browns Bank in 1985. The Browns Bank data were selected since they represented the largest regional data set ($N = 507$ for cod; $N = 545$ for haddock) and the broadest temperature range through the time series: 3–11°C.

The fit of the model initially appeared to be quite good ($R^2 = 0.93$ and 0.81 for cod and haddock, respectively), but examination of the residuals as a function of age indicated that the model seriously overestimated the length of larvae older than 90 d. Accordingly, the model was altered to reflect a more realistic growth form, the logistic equation, in conjunction with a linear temperature interaction. The fit of this model was better than that of model (3), but persistant patterns in the residuals were identified among the older larvae of the February cruise (H130) and the younger larvae of the June cruise (H137). Since these two sets of larvae would have experienced the highest temperatures of the sampling season (>10°C), it is likely that such temperatures would have exceeded the larval growth optimum. Temperature optima are well documented in temperate fishes (see review by Brett (1979)) and would be expected in cod and haddock stocks nearing the southern limit of their range. Growth–temperature optima were modelled in this study through use of a quadratic parabola, which has been used successfully in many other studies of fish growth (Ricker 1979). The parabolic temperature term was initially incorporated into a modification of model (3); allying exponential growth (the most parsimonious model) with an inverse parabolic temperature term, the latter served to increase absolute growth rate parabolically to a temperature-based optimum, after which growth rate decreased.

The fit of this model was again good for both species, but it produced trends in the residuals for the oldest larvae. These results suggested that the temperature parabola was effective, but that exponential growth could not be assumed in older fish. Accordingly, the latter two models were merged to incorporate both logistic growth and a parabolic temperature interaction, resulting in

$$L_{age} = L_{hatch} + K \int_{t=0}^{age} \frac{\text{d(logistic)}}{dt} \cdot (c - (T_t - T_{opt})^2) dt$$

and the numerical approximation:

$$(4)\quad L_{age} = L_{hatch} + K \sum_{t=0}^{age} (Gl_t - Gl_t^2 L_\infty^{-1})\,(c - (T_t - T_{opt})^2),$$

where $l_t = L_\infty(1 + \exp(-G(t-t_0)))^{-1}$; $G$, $L_\infty$, $t_0$, $c$, and $T_{opt}$ (= temperature optimum) are model parameters; and $L_{hatch}$ and $K$ are fixed at 3.0 and 0.2, respectively. While the fixed value of $L_{hatch}$ was somewhat arbitrary, model results were insensitive to the specific value within the range of 2–5 mm. The fit of this model to the aggregated Browns Bank data was excellent ($R^2 = 0.96$ and 0.83 for cod and haddock, respectively) and appeared to be unbiased across all combinations of cruise, length, and age (Fig. 5; Table 7). The fit was particularly good for the cod larvae, and given the range of months, temperatures, ages, and lengths present in the data, it would appear to be a robust predictor of larval length. Use of five different cruise collections in the test data set precluded any collinearity between temperature and age. Of course, the predictive power of any model decreases near the extremes of the data range, and this effect is to be particularly expected for the largest cod larvae; the potential for avoidance of the bongo gear is almost certainly present in larvae >10 mm (I. Suthers, Department of Biology, Dalhousie University, Halifax, N.S., pers. comm.) and would be expected to result in preferential capture of the slower growing individuals. It is unlikely that gear avoidance had a significant effect upon the size-at-age estimates of the much smaller haddock larvae. However, the restricted ranges of the haddock age, length, and temperature data constrained the utility of the growth model to larvae less than 35–40 d old.

The predictive capability of the model was assessed through tests with independent data sets. Growth projections for cod and haddock on Browns and Georges banks in 1984, and on Georges Bank in 1985, were made using the parameters in Table 7, resulting in predictions similar to those actually observed; in all cases, the mean residual was approximately 0. Slight trends were observed in the residual patterns of cod from cruises H116 (1984; Browns) and H135 (1985; Georges), and in haddock from H114 (1984; Georges), but the source of the discrepancy was difficult to pinpoint. There is no question that imprecision in the estimated temperature record could have resulted in the predicted growth anomalies; simulations with the temperature data verified this. An equally viable explanation is the absence of food availability/consumption as a term in the growth model. Since food consumption is known to influ-

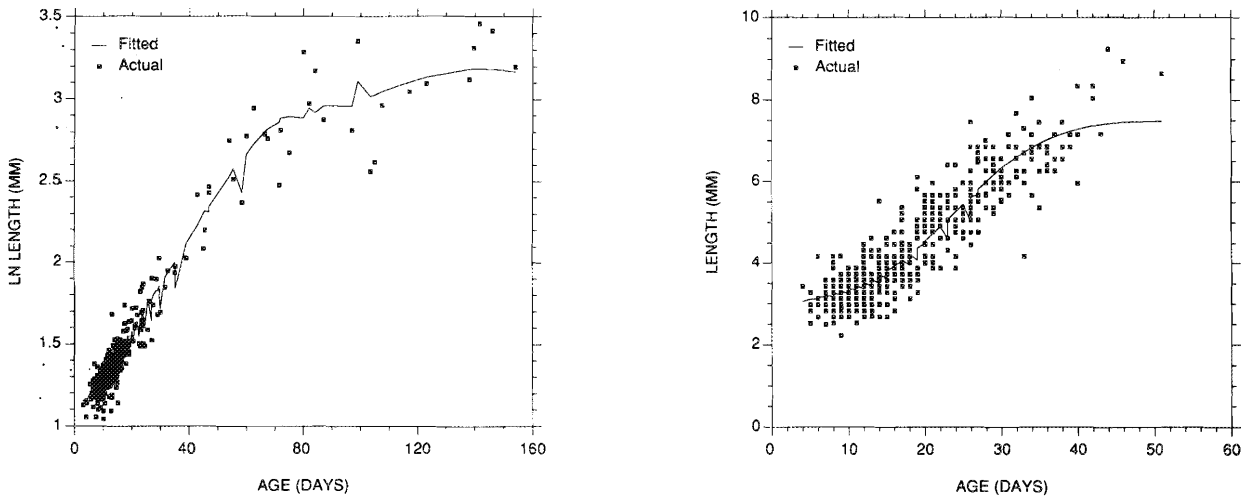


FIG. 5. Fit of an age- and temperature-mediated growth model (equation (4), described in text)) to cod (left) and haddock (right) larvae on Browns Bank in 1985. Data were aggregated across cruises. The model assumes logistic growth and a parabolic relationship between temperature and absolute growth rate on a daily basis. The fitted line appears irregular since only one of the two independent variables is plotted. Model results are summarized in Table 7.

TABLE 7. Parameter estimates, associated error terms, and ANOVAs for a model integrating logistic growth and a parabolic temperature term in the estimation of larval length (see model (4) in text). The model was fit to both cod (ln-transformed) and haddock (untransformed) data collected on and around Browns Bank in 1985.

| Species | Source of error | Sum of squares | *df* | Mean square | $R^2$ | Parameter | Coefficient | SE |
|---|---|---|---|---|---|---|---|---|
| Cod | Model | 875.81 | 5 | 175.16 | 0.96 | $G$ | 0.05016 | 0.00274 |
| | Error | 3.2169 | 357 | 0.00901 | | $L_\infty$ | 59.18 | 13.44 |
| | | | | | | $t_0$ | 60.57 | 2.33 |
| | | | | | | $c$ | 22.77 | 4.44 |
| | | | | | | $T_{opt}$ | 5.925 | 0.195 |
| Haddock | Model | 11047 | 5 | 2209.5 | 0.83 | $G$ | 0.1571 | 0.0110 |
| | Error | 158.02 | 539 | 0.29318 | | $L_\infty$ | 5.467 | 5.081 |
| | | | | | | $t_0$ | 24.44 | 0.89 |
| | | | | | | $c$ | 44.00 | 39.79 |
| | | | | | | $T_{opt}$ | 6.701 | 0.936 |

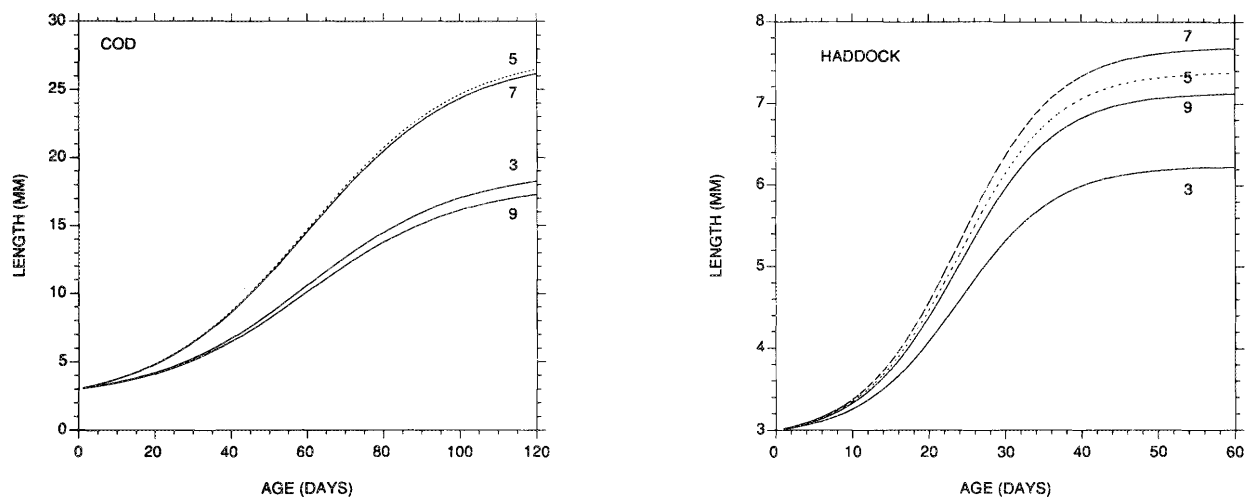


FIG. 6. Growth projections for cod and haddock larvae at various constant temperatures as predicted from model 4 (described in text). Digits refer to the temperature in degrees Celsius.

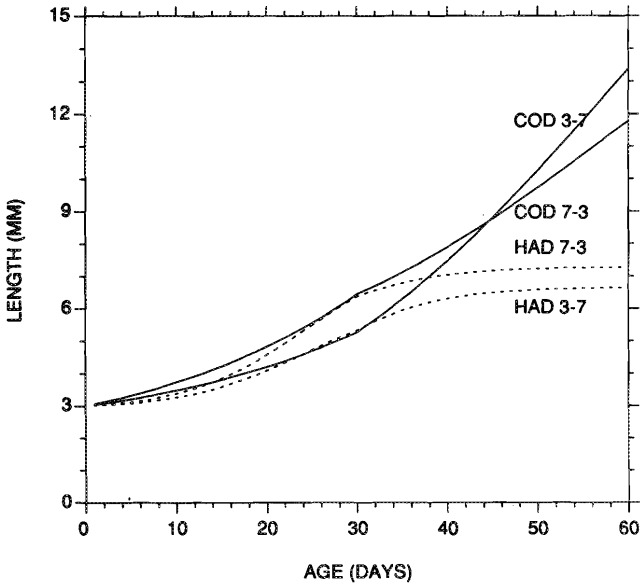


FIG. 7. Growth projections from model 4 (described in text) for cod and haddock larvae under interrupted temperature regimes. Temperature was held constant at one temperature (3° or 7°C (first digit in label)) for 30 d, following which it was shifted to a second temperature (3° or 7°C (second digit in label)) for the remaining 30 d. Temperature had the most sustained effect on growth when absolute growth rate was greatest.

ence the growth of larval cod and haddock (Laurence 1974; Laurence et al. 1981; Ellertsen et al. 1981), food availability may differ enough spatially and temporally to introduce error into the model projections. It is important to note however, that the model residuals from five independent data sets were invariably small, and equally explicable in terms of prey concentration or temperature anomalies. Given the level of precision required here, and the close correspondence between temperature and prey abundance in many ecosystems, the distinction between these latter two factors may be irrelevant in the context of this model.

## Comparative Growth of Cod and Haddock Larvae

The logistic form of the growth equation used here has been fitted to length-at-age data from a wide variety of other species (Bailey 1982; Nishimura and Yamada 1984; Boehlert and Yoklavich 1985; Crecco and Savoy 1985; Warlen and Chester 1985). With the incorporation of the temperature term as a function of absolute growth rate, temperature becomes a significant modifier of growth rate. Growth was optimized at a specific temperature in both species, in keeping with the parabolic form of the temperature terms (Fig. 6). The greater optimal temperature ($T_{opt}$) for haddock (6.7°C) over that of cod (5.9°C) is consistent with the distribution of each species along the eastern coast of North America.

Temperature exerted its most significant effect upon growth at the inflection point of the growth curve, where the rate of growth was most rapid. In the case of haddock, this occurred at an age of 20–30 d; the inflection point for cod was somewhat later (40–50 d). The influence of an age-structured temperature–growth rate relationship was demonstrated in growth projections where temperature was held constant at 3°C until age 30 d, after which it was shifted to 7°C until age 60 d; the converse temperature shift did not result in a comparable length at age 60 d, despite the equivalent number of degree–days in each 30-d interval, because of the higher size-structured growth rates in the older larvae (Fig. 7).

A comparison of the growth projections for each species indicates that neither has a substantial growth advantage within the temperature range of 3–7°C, at least until the age of 30 d (Fig. 6). After that age, haddock growth rate was reduced relative to that of cod, resulting in significant differences in size at age 50 at all temperatures. The inter-specific comparability of the growth curves noted here for young larvae is similar to that reported on Georges Bank (Bolz and Lough 1983; Buckley and Lough 1987) and in the laboratory (Laurence 1978). However, the divergence of the growth curves after approximately age 30 d is inconsistent both with Bolz and Lough's (1983) field study and with Laurence's (1978) laboratory work. Interestingly, a later study by Laurence (1981), in which cod and haddock larvae were forced to compete for food resources, produced an inter-specific growth divergence nearly identical to that reported here. Laurence (1981) discussed possible mechanisms for the divergence, including cannibalism, predation on haddock by cod, and prey size selectivity. Neither of our studies were designed to test among these hypotheses, but the similarity in results between his laboratory experiment and our field study is striking.

Predicted length-at-age values from our model are 30–40% less than those reported for Georges Bank by Bolz and Lough (1983). While the latter did not test for potential resolution losses in their interpretation of the otolith microstructure, our results indicate that these losses would have introduced little error into either of our estimates of age. The remaining procedural difference between the two studies was that associated with the measurement of larval length: Bolz and Lough (1983) applied Theilacker's (1980) shrinkage correction equation to all of their length data, while we did not. On the assumption that the observed cod lapillus diameter: larval length relationship was similar in both studies (Campana 1989), and given the resistance of lapilli to deformation/shrinkage, the observed lapillus diameters were used to calculate a common frame of reference for length between the studies. When Theilacker's (1980) equation was then applied to the standardized data, our prediction of cod larval length at the temperatures reported by Bolz and Lough (1983) fall within 3% of their estimates. While the consistency between the two independent growth estimates is remarkable, the question remains of whether or not to calculate growth on the basis of preserved or adjusted lengths. An unbiased estimate of live length would certainly be preferable. However, Theilacker's (1980) equation was designed for use with anchovy (*Engraulis mordax*) larvae, whose shape differs substantially from that of cod and haddock. It also results in cod shrinkage estimates on the order of 30%, which appears to be unreasonably high compared to the ~10% reported for silver hake (*Merluccius bilinearis*) larvae (Fowler and Smith 1983). Given the morphological similarity between larval silver hake and cod/haddock, we feel that a shrinkage estimate of ~10% is more representative of gadids. However, in the absence of a valid predictive equation for shrinkage, we have left our growth predictions uncorrected, in the knowledge that adjustments can always be made after the appropriate calibrations have been conducted.

Aside from the study of Bolz and Lough (1983), there are few studies with which to test the generality of our growth model. Anderson's (1982) growth rate calculations for cod were length- rather than age-structured, but our estimates of growth rate from his data were consistent with those that he estimated

for Flemish Cap. Laboratory estimates of growth rate do not necessarily reflect those obtained in the field, but in the case of Laurence's (1981) cod and haddock data, they do. Similarly, using the temperatures and ages reported by Ellertsen et al. (1981), our predictions of cod length at ages of 30–50 d were consistent with those (± 10%) actually measured in two of their three enclosures; their third, high-food density enclosure supported growth rates considerably higher than those predicted by our model. Therefore, we conclude that the age- and temperature-based growth model developed here accurately reflects the growth of larval cod and haddock over a broad range of environmental conditions, but requires modification if it is to deal with extended, anomalous food conditions. Such conditions were not encountered in seven independent larval collections in the Gulf of Maine.

## General Discussion

Process-oriented growth models derived from experimental results serve a useful function as vehicles for hypothesis testing. However, studies reporting the growth of wild marine larvae have made almost exclusive use of simple age–length regressions, in apparent disregard of the more sophisticated models developed elsewhere (Bolz and Lough 1983; Beckman and Dean 1984; Nishimura and Yamada 1984; Walline 1985; Leak and Houde 1987). This situation reflects not so much the inapplicability of the alternative models, as the difficulty associated with their parameterization. Parameters are particularly difficult to estimate for terms associated with feeding and behaviour. Yet, in addition to age, feeding and temperature are the two variables most influential in determining larval growth (Vlymen 1977; Laurence 1978; Ellertsen et al. 1981; Laurence et al. 1981; Taniguchi 1981; Buckley 1984; Crecco and Savoy 1985). As a result, age–length regressions perform well as growth descriptors for a specific study, but lack applicability to other water masses, seasons, and populations.

In this paper, we hope to have bridged some of the gap between theory and application, through presentation of a generic larval growth model with a number of advantages over existing formulations. The advantages include: (1) conceptual soundness; the influence of age and temperature upon growth rate is well documented in both the theoretical and the empirical literature; (2) ease of parameterization; age-structured data can now be routinely collected through otolith microstructure techniques in a wide variety of species. Temperature data are easy to collect, either through hydrographic sampling or remote sensing observations. Since foraging data are difficult both to collect and to interpret, a feeding term has intentionally been omitted from the model; and (3) the potential for application of the model to a wide variety of environmental regimes, populations, and even species.

The robustness of any model will inevitably depend upon the nature of the inherent assumptions, and how well they are met. In this study, the assumption that otolith microstructure examination provided an accurate index of age was tested both through validation experiments and tests for inadequate resolution of narrow increments. The former were consistent with previous reports of daily increment formation in larval cod (Radtke and Waiwood 1980; Bergstad 1984; Dale 1984) in that increments formed daily in all but the early larval stage; the resolution limitations of light microscopy were almost certainly responsible for the poorer increment–age correlation among the youngest larvae. Age underestimation of the Gulf of Maine larvae was less than or equal to the magnitude of that in the laboratory, implying a minimal bias. However, the bias would be expected to be more severe in slower growing populations (Campana et al. 1987).

A second model assumption was that sea surface temperature (SST) adequately characterized the temperature environment of the larvae. Cod and haddock larvae are generally concentrated in the upper 30 m of the water column, above the thermocline (Tilseth and Ellertsen 1984; Ellertsen et al. 1984; Fridgeirsson 1984), where SST adequately reflects the temperature regime. Of course, neither day-to-day temperature anomalies nor small scale spatial variations are reflected in the smoothed temperature record used here. However, given the fact that the drift path of individual larvae was also unknown, the temperature model provided a useful integration of temperature at the daily level.

The final assumption concerned the validity of the model formulation. Yet the empirical basis for a growth–temperature interaction in cod and haddock larvae is so strong that only the omission of such a term should have to be justified. The advantage of incorporating the temperature term at the daily level was the elimination of the need for broad estimates of the mean temperature experienced by a sample of larvae. While a posteriori tests for temperature effects have been successful in some instances (Crecco and Savoy 1985), there have been other studies where the explicit incorporation of a temperature term in the growth model may have proven more effective (Methot and Kramer 1979; Jones 1985; Walline 1985; Leak and Houde 1987). A secondary benefit of the temperature term was the apparently-reduced requirement for a feeding term. While an explanation for this is not yet clear, feeding effects upon growth should become evident in the model residuals, thus providing an index of relative food availability through the study period.

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