

# Spatial implications of a temperature-based growth model for Atlantic cod (*Gadus morhua*) off the eastern coast of Canada

S.E. Campana, R.K. Mohn, S.J. Smith, and G.A. Chouinard

**Abstract:** Lengths at age of Atlantic cod (*Gadus morhua*) off the eastern coast of Canada vary up to three-fold among geographic regions, with Georges Bank and the southern Gulf of St. Lawrence being the regions of fastest and slowest growth, respectively. Colour-coded contour maps of length at ages 2–8 ( $n = 59\,518$ ) based on research vessel surveys between 1971 and 1992 clearly showed the spatial variations in size at age. Corresponding maps of July–September bottom water temperature appeared to reflect relative growth rate, whereas those for depth did not. A polynomial expansion of a temperature-based von Bertalanffy growth model appeared to fit the data well, with no residual patterns across most ages, lengths, temperatures, or years. Model predictions were also consistent with reported lengths at age for cod in other regions and countries. Declines in bottom water temperature over the past 5–10 years appear to be at least partly responsible for observed declines in size at age of the cod stock on the eastern Scotian Shelf.

**Résumé :** La longueur selon l'âge de la morue Atlantique (*Gadus morhua*) sur la côte est du Canada varie par un facteur pouvant aller jusqu'à trois fois entre les différentes régions géographiques. Le Banc Georges constitue la région de croissance la plus rapide alors que le sud du Golfe du St. Laurent est celle de croissance la plus lente. Des cartes couleur des isolignes de la longueur selon l'âge pour les poissons de 2 à 8 ans ( $n = 59\,518$ ) obtenues des relevés scientifiques de 1971 à 1992 montrent clairement la variation spatiale de la taille selon l'âge. Les cartes correspondantes des températures au fond en juillet–septembre semblent correspondre au taux relatif de croissance contrairement à celles de la profondeur. Le développement polynomial d'un modèle de croissance de type von Bertalanffy basé sur la température a donné un bon ajustement des données, sans tendance évidente des résiduels pour la plupart des âges, longueurs, températures ou années. Les prédictions du modèle sont aussi en accord avec les tailles selon l'âge pour d'autres régions et d'autres pays. Selon une autre version du modèle, le déclin de la taille selon l'âge pour la section est du Plateau Néo-Écossais semble être du, au moins en partie, au déclin des températures au fond sur cette zone au cours des 5 à 10 dernières années.

## Introduction

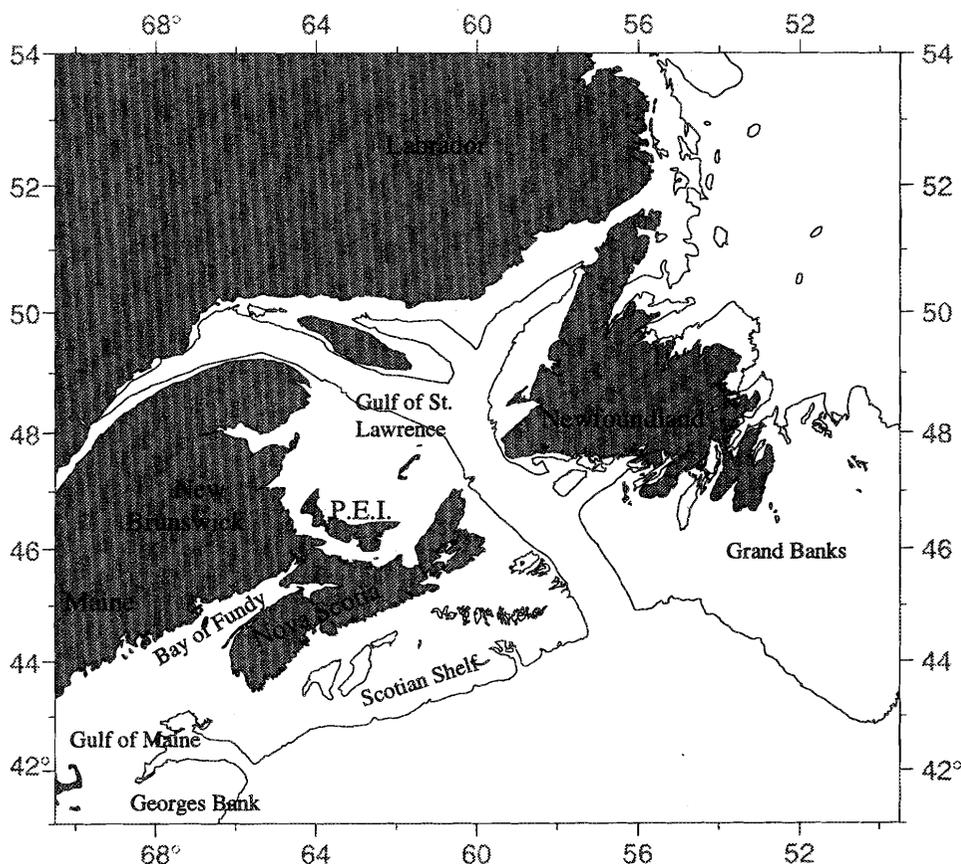
Length at age in fish is often highly variable, with the degree of variability increasing with age. For physiological reasons, this observation is expected; fish growth varies with differences in temperature, food consumption, size, and genetic strain, as well as other factors (Brett 1979; Ricker 1979), with the resulting size differences being cumulative with age. As a result, bioenergetics models have had some success in predicting fish length and (or) weight under given environmental conditions (e.g., Madenjian and Carpenter 1991; Arnason et al. 1992). Unfortunately, bioenergetic parameter estimates and measures of food consumption are seldom

available in field situations, necessitating an alternative approach. Linear models incorporating environmental terms provide such an alternative (Maccina 1992; Millar 1992; Weisberg 1993) but are more limited in terms of their predictive capabilities. They also fail to take advantage of any spatial patterns in size at age that may exist in the study area (Brandt and Kirsch 1993). Therefore, there appears to be a need for an easily parameterized growth model with predictive capabilities that can be mapped to show large-scale geographic patterns in size at age.

Numerous anecdotal reports have noted large geographic differences in size at age among Atlantic cod (*Gadus morhua*) stocks off the northeastern coast of North America. For example, cod on Georges Bank are widely known for their apparently rapid growth rate, whereas cod from the Gulf of St. Lawrence are equally well recognized for being among the slowest growing of the Atlantic cod stocks. Furthermore, there is considerable spatial heterogeneity in size at age within stocks. For instance, cod caught in research vessel (RV) surveys near the mouth of the Bay of Fundy are consistently larger at age than those on the

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**Fig. 1.** Map of the study area showing the 200-m bathymetric contour.

offshore banks of Northwest Atlantic Fisheries Organization (NAFO) division 4X, despite the fact that both areas are part of the same stock assessment unit (Campana and Hamel 1992). While regional and temporal variations in cod growth have variously been attributed to the effects of food (Kohler 1964; Braaten 1984), fishing (Hanson and Chouinard 1992), and temperature (Taylor 1958; Jorgensen 1992; Brander 1995), there have been few large-scale examinations of cod growth that incorporate both within-stock and across-stock differences in size at age (but see Brander 1995).

The objectives of this study were to document the large-scale gradients in cod size at age in the southern Gulf of St. Lawrence, the Scotian Shelf, and the Gulf of Maine (Fig. 1) and to develop a simple age-temperature growth model that was consistent with decadal-scale spatial patterns in both size at age and temperature. We conclude by using the model to estimate the impact of long-term cooling on the relative size of cod on the eastern Scotian Shelf.

## Materials and methods

### Data preparation

All size at age data were derived from RV surveys rather than the commercial fishery to avoid complications resulting from long-term changes in the size selectivity of fishing gear. Length, age, bottom water temperature, and depth data were obtained from July RV surveys conducted by

the Department of Fisheries and Oceans for the Scotian Shelf and Georges Bank through the period 1971–1992. The corresponding data from the southern Gulf of St. Lawrence were obtained from September RV surveys. Use of a 19-mm mesh liner in the cod end reduced the probability of any fish extrusion through the net. However, analysis was also restricted to ages 2–8 to minimize the possibility of size-selective availability to the gear throughout the survey region. All cod were measured to the nearest centimetre, and otoliths for age determination subsampled from up to 3 fish per 3-cm length interval in each set (1 fish per 1-cm interval in the Gulf of St. Lawrence since 1985). Estimates of mean length at age for a given set were left unweighted by length frequency because there was little appreciable difference between weighted and unweighted estimates; the slope relating the weighted and unweighted estimates was 0.99, and discrepancies at age were <5%.

The cod length at age data were examined in two ways: using colour-coded contour maps for a visual assessment of spatial pattern and through statistical analysis. The two approaches were intended to complement each other, the first providing an easily grasped overview and the second providing the statistical rigour. However, it is important to note that all hypothesis testing was restricted to the statistical analysis.

Colour-coded contour maps were contoured using Delauney triangles (Watson and Philip 1985) of set-by-set

data averaged over 0.2° squares. Interval scales were extended over the entire range of the data. Because the contour maps were prepared solely for the purpose of assessing spatial pattern, data were aggregated into 11- or 12-year blocks for each map. Visual comparisons between time blocks were then made as assessments of long-term shifts in size at age or temperature.

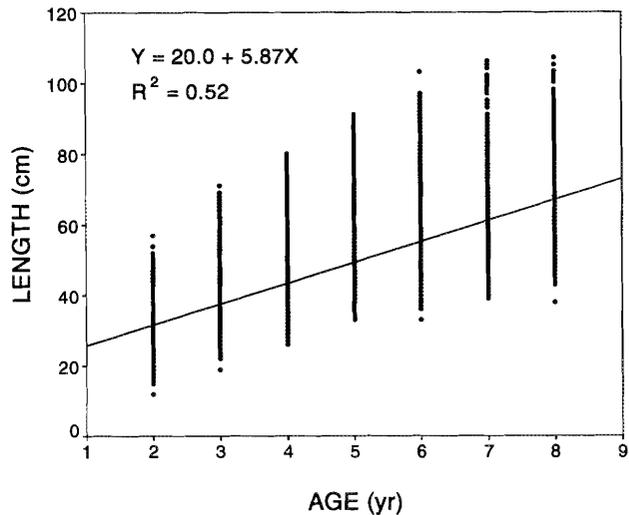
The cod growth model was designed to give equal weight to all geographic regions, irrespective of fish density. Accordingly, a single estimate of mean length at age was calculated for each 0.5° square for each 5- or 6-year time period, on the basis of a mean data density of about 20 observations per cell. Mean temperatures at age were based only on temperatures associated with the capture of cod. While it is unreasonable to assume that temperature at capture represents ambient temperature at earlier ages, this assumption was necessary because of our inability to reconstruct the temperature history of individual fish. Plots of temperature-at-capture versus age and (or) size differed substantially among the five cod stocks (Page et al. 1994; this study) demonstrating that there was no consistent age- or size-related temperature preference. For instance, young cod on the eastern Scotian Shelf and in the Gulf of St. Lawrence tended to be found in warmer water than did older cod, although there was no such tendency off southwestern Nova Scotia or on Georges Bank. While mean annual bottom water temperatures at each site would have been preferred for use as an index of annual temperature exposure by cod, such were not available. Accordingly, we considered it important to use temperature measurements that would not be unduly influenced by short-term seasonal fluctuations. Since bottom water temperatures at shallow stratified sites are more seasonally variable than those at deepwater and well-mixed sites, all collections made at stations of <50 m depth were excluded from subsequent analysis.

**Model development**

On the basis of known biological principles, there were three features that we thought important to capture in a growth model: inclusion of a temperature term, a gradual reduction in relative growth rate with increasing age, and increasing variance in length at age with age. All of these objectives could conceivably be met through modifications to the von Bertalanffy growth model. As noted by Beverton and Holt (1957), the von Bertalanffy growth model would be expected to reflect the influence of temperature through its effect on the parameter *K*. Of the two von Bertalanffy model formulations that have been developed to incorporate a seasonal temperature effect, one is based on the definition of a temperature-based growing season (Pitcher and MacDonald 1973), while the other models the parameter *K* as a smooth and cyclic function of temperature and time (Ursin 1963; Pawlak and Hanumara 1991).

Our interest was in empirically testing for the effect of temperature on the parameters of the von Bertalanffy model. Model building, testing, and diagnosis can be problematic for nonlinear models such as the von Bertalanffy. Therefore, we chose to model growth as a linear function to take full advantage of the diagnostic tools that have been developed for linear models. That is, instead of using

**Fig. 2.** Linear regression of length on age for all age 2–8 cod collected between 1971 and 1992.



$$[1] L_{age} = L_{\infty} (1 - \exp(-K(\text{age} - t_0)))$$

where  $L_{age}$  is length at age, and  $L_{\infty}$ ,  $K$ , and  $t_0$  are parameters to be estimated, we used a Taylor series expansion of the nonlinear model (see Beverton and Holt 1957, p. 99) to get

$$L_{age} = \beta_0 + \beta_1(\text{age}) + \beta_2(\text{age})^2 + \beta_3(\text{age})^3 + \dots + \beta_n(\text{age})^n$$

The corresponding terms from the Taylor series expansion are given as

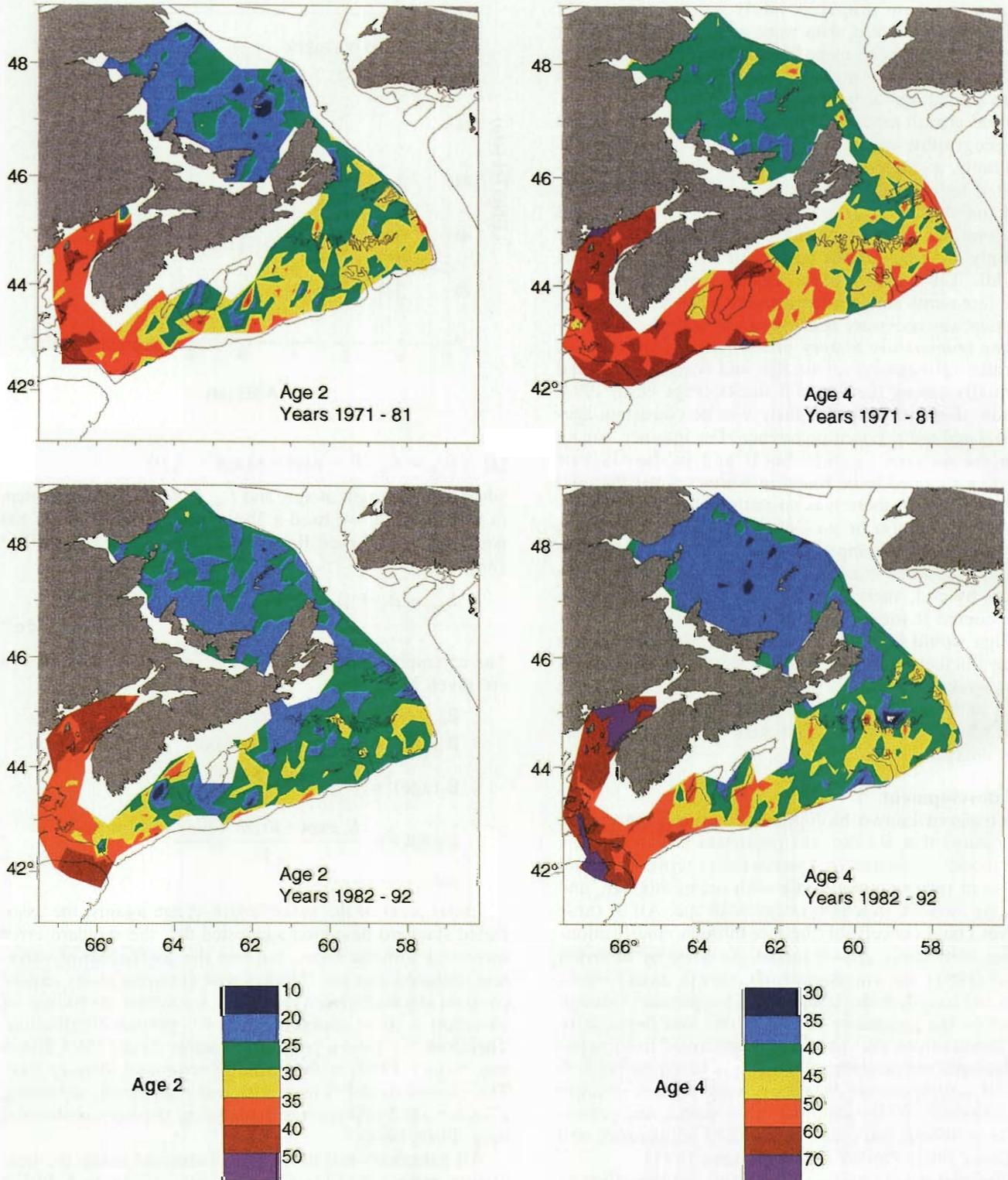
$$\begin{aligned} \beta_0 &= L_{\infty}(1 - \exp(-Kt_0)) \\ \beta_1(\text{age}) &= L_{\infty}\exp(-Kt_0)K(\text{age}) \\ \beta_2(\text{age})^2 &= \frac{-L_{\infty}\exp(-Kt_0)K^2(\text{age})^2}{2} \\ \beta_3(\text{age})^3 &= \frac{L_{\infty}\exp(-Kt_0)K^3(\text{age})^3}{6} \end{aligned}$$

etc.

Initial plots of the mean length at age against the associated standard deviation suggested that the standard error increased with the mean, but that the coefficient of variation remained constant. Models with Gaussian errors require constant standard error (variance). A constant coefficient of variation is more characteristic of a gamma distribution. Therefore, we used a generalized linear model (McCullagh and Nelder 1989) with a gamma error and identity link. The gamma model is more efficient than simply assuming a lognormal distribution and analyzing the log-transformed data (Firth 1988).

All parameter estimates were estimated using the iteratively reweighted least-squares algorithms in S-PLUS (STATSCI 1993). Temperature was included in the model as a simple additive term and as an interaction term with each of the age polynomial terms. The significance of all terms in the model was tested using the analysis of deviance approach and  $\chi^2$  test discussed in McCullagh and Nelder (1989).

**Fig. 3.** Colour-coded contour maps of cod showing spatial patterns in relative size (cm) at each of four ages (ages 2, 4, 6, and 8) and two periods (1971–1981 and 1982–1992). The 200-m bathymetric contour is indicated.

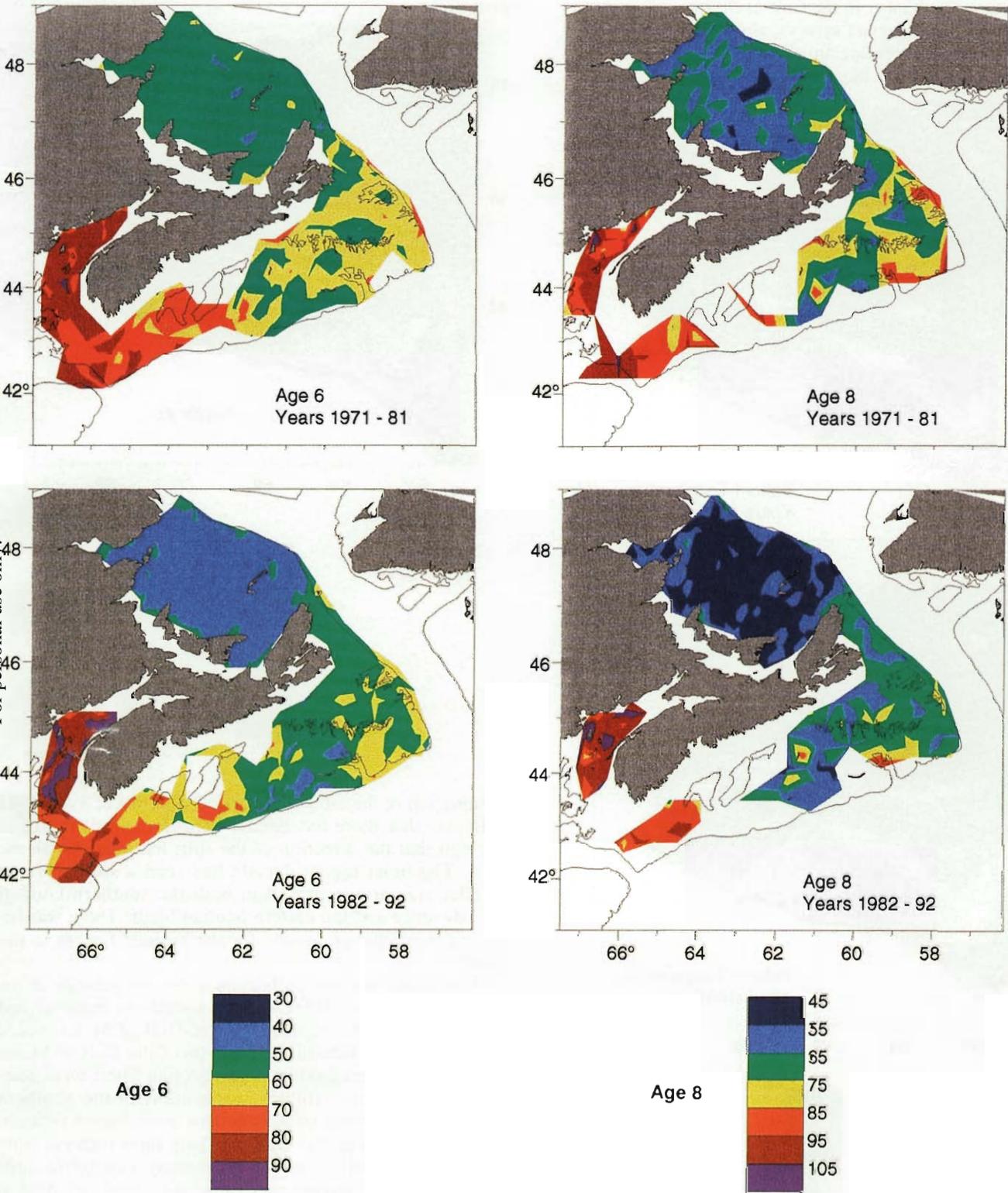


**Results**

A total of 59 518 cod length at age observations were collected between 1971 and 1992. A simple regression of length on age highlighted the expected increase in variance with age

and relatively low explained variance (52%) (Fig. 2). However, the distribution of the regression residuals was clearly nonrandom across ages, predicted values, and stocks, indicating that a simple regression was unsuitable for describing these data. When viewed as colour-coded contour maps

Fig. 3 (concluded).

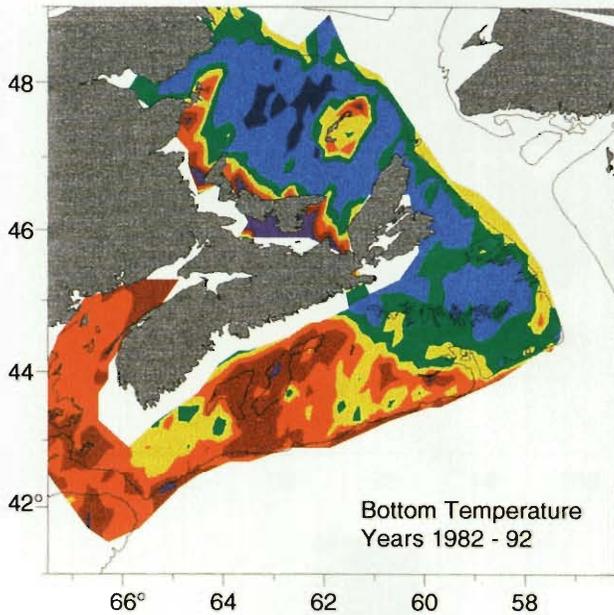
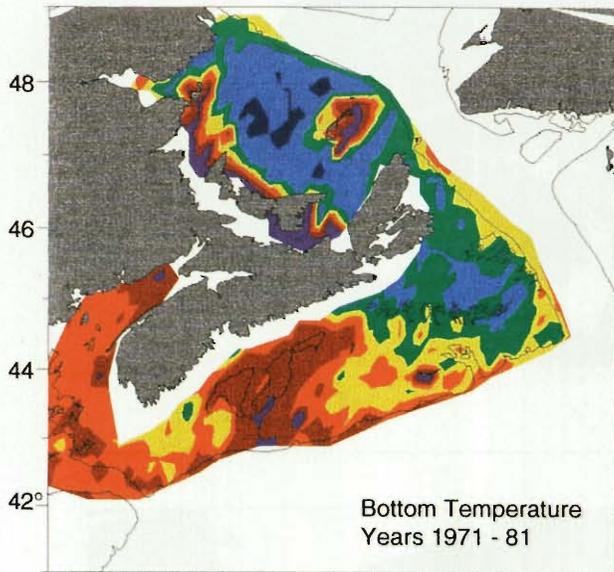


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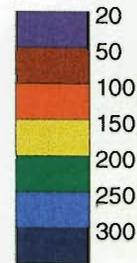
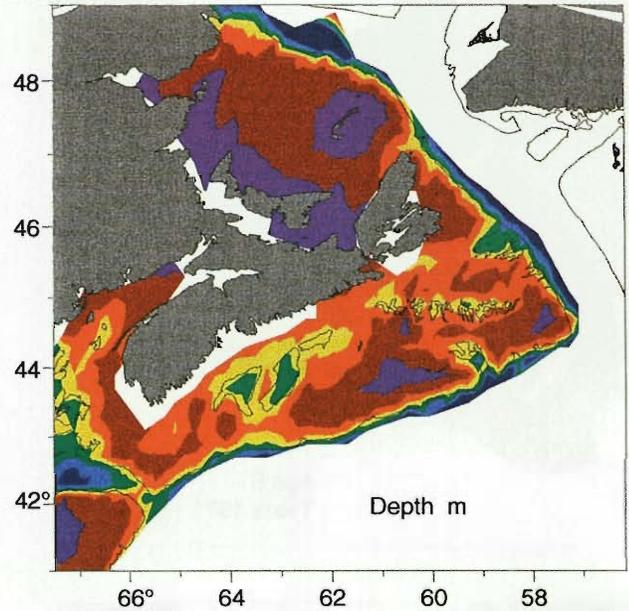
(Fig. 3), the relative size of cod at each age varied substantially and coherently among regions, thus explaining at least part of the variability in the length–age regression. Indeed there was at least a three-fold difference in size at age between cod from the southern Gulf of St. Lawrence

and Georges Bank at all ages. In general, size at age decreased from north to south along the Scotian Shelf, although the decline was not clearly linked to latitude: cod in the Bay of Fundy were up to 50% larger than their counterparts at the same latitude on the Scotian Shelf.

**Fig. 4.** Colour-coded contour maps of July bottom water temperatures (September in the Gulf of St. Lawrence) as recorded in research vessel surveys, along with the 200-m bathymetric contour. Temperatures (°C) represent all those recorded, not just those associated with cod catches.



**Fig. 5** Colour-coded contour map of depth (m) in the study area.

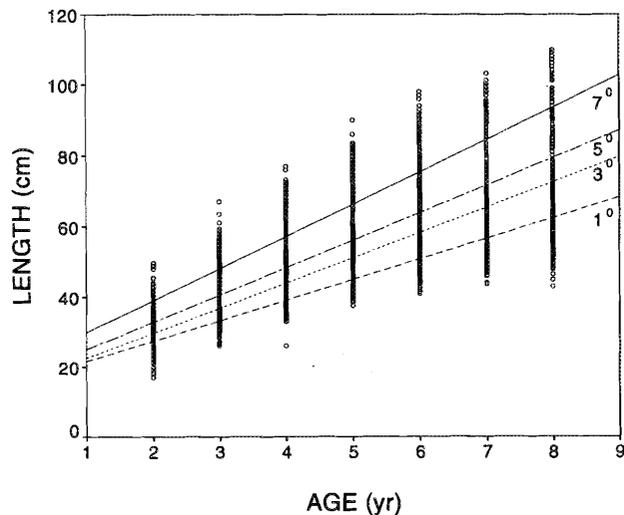


Comparison of the 1971–1981 period with that of 1982–1992 indicates that there has been a long-term shift in size at age and that the direction of the shift has varied with the area. The most recent decade has seen a shift towards smaller size at age of cod in both the southern Gulf of St. Lawrence and the eastern Scotian Shelf. There was little apparent change in size for the regions further to the south.

The spatial patterns of bottom water temperature at the time of the survey (Fig. 4) were similar to those of cod size at age. In general, the southern Gulf of St. Lawrence was relatively cold, while the waters of the Gulf of Maine and the deepwater basins of the Scotian Shelf were relatively warm. Anomalously warm areas in the southern Gulf of St. Lawrence were associated with shallow (<50 m) stratified sites (Fig. 5), thus justifying their removal from the growth modelling section of the study. Long-term shifts in bottom water temperature were not clearly evident at the decadal level of comparison (Fig. 4), although comparisons of 5-year periods showed that the Gulf of St. Lawrence and eastern Scotian Shelf cooled during the mid to late 1980s.

Temperature was a significant covariate of length at any given age (ANCOVA,  $p < 0.001$ ). When aggregated by 2° intervals, temperature was associated with an apparent

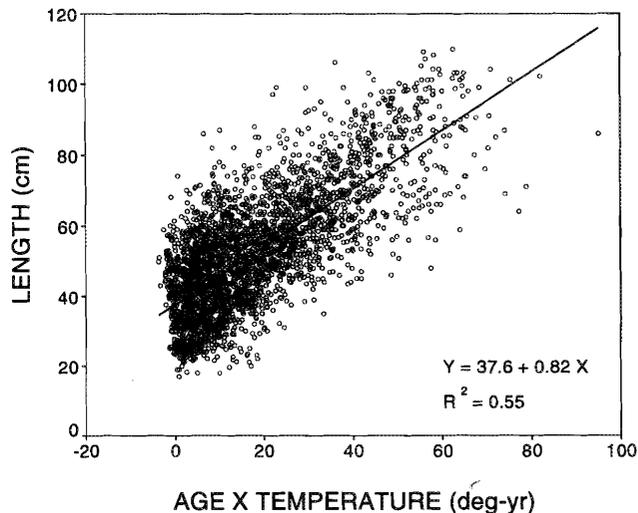
**Fig. 6.** Relationship between length and age of cod when weighted uniformly by geographic area (see Methods). Solid lines represent regression lines fitted to 2° temperature categories, indicating an apparent increase in growth rate associated with an increase in temperature.



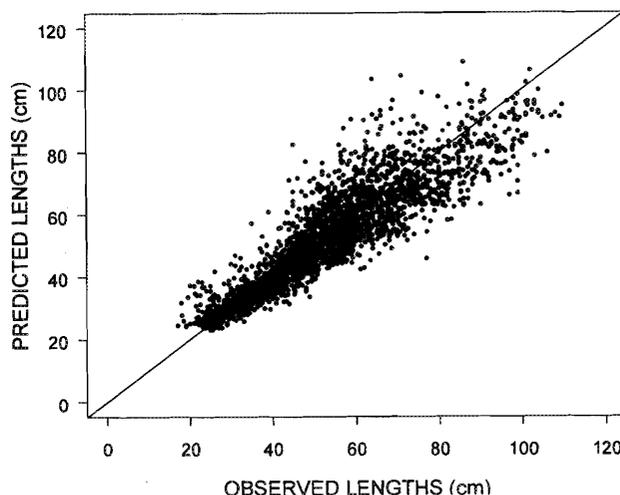
increase in growth rate of cod (Fig. 6). To determine if the relationship could be explained as simply as through the use of cumulative growing years, degree-years (based on a point estimate of temperature for each year) were regressed on length (Fig. 7). The relationship was highly significant but explained no more of the variance than did the simple regression of age on length. In addition, the residuals were not distributed randomly across ages, years, temperatures, or stocks. Thus, such a simple model was not sufficient to explain much of the observed variability in cod size at age.

A Taylor expansion of the modified von Bertalanffy equation using a gamma error provided a much better fit to the length at age data than did the simpler models considered previously. Only the lower order terms of the Taylor expansion proved to be statistically significant. All possible submodels were tested against the full model defined as having a second-order polynomial in age, with temperature as a main effect and included in interaction with all of the age terms. The best submodel was a simple model of  $L = 1 + \text{age} + \text{temperature} + \text{age} \times \text{temperature}$  (Table 1). However, when tested against a third-order version of the same full model, the best submodel lacked a significant age  $\times$  temperature interaction term (Table 1). There was no objective means for selecting between these two submodels. Therefore, we initiated an empirical forward-stepping model fitting procedure, in which the same set of age and temperature terms described above were added hierarchially to a simple mean model, along with a stock term. The resulting set of significant terms included all of those derived from the Taylor expansion quadratic submodel described above but with the addition of a significant stock term (Table 2). Therefore, the submodel resulting from the quadratic model was accepted as best, while the stock effect in Table 2 was interpreted as a reflection of geographic differences in temperature seasonality. Parameter

**Fig. 7.** Linear regression of length on the product of age and temperature (degree-years). While statistically significant, this regression did not explain appreciably more of the variance than did the regression of length on age.



**Fig. 8.** Observed versus predicted values of cod length at age based on a Taylor expansion of a temperature-based von Bertalanffy growth model. The deviance residuals of the model were randomly distributed across all predicted values, time periods, temperatures, and ages, with the exception of the very smallest and largest fish. The 1:1 line is indicated.



estimates for the age, temperature, and age  $\times$  temperature terms in the Taylor expansion and forward-stepping models were similar, despite the additional presence of the stock term in the latter model. Temperature  $\times$  stock interactions were also significant, reflecting the different patterns of temperature seasonality in the different stocks. No obvious patterns were evident in the residual plots from the Taylor expansion submodel, with the exception of size underestimation of the largest fish (Fig. 8).

Geographic variations in the degree of model fit were viewed by mapping the deviance residuals at age (Fig. 9).

**Table 1.** Hierarchical screening of terms for the Taylor expansion of the temperature-based von Bertalanffy growth model and parameter estimates resulting from the accepted quadratic submodel.

Terms	df	Deviance	P value	
			Cubic	Quadratic
Full model (cubic)	2923	47.681	—	—
Full model (quadratic)	2925	47.796	—	—
Reduced models				
Age <sup>3</sup> × temperature	2924	47.775	0.759	—
Age <sup>3</sup>	2925	47.796	0.943	—
Age <sup>2</sup> × temperature	2926	47.808	0.988	0.916
Age <sup>2</sup>	2927	50.669	0.559	0.238
Age × temperature	2928	57.765	0.073	0.007
Temperature	2929	124.122	<0.001	<0.001
Age	2930	335.683	<0.001	<0.001

Parameter estimates resulting from the accepted quadratic submodel

Parameter	Coefficient	Standard error
Intercept	13.08	0.393
Age	5.84	0.092
Temperature	0.56	0.098
Age × temperature	0.51	0.024

**Note:** The full cubic model is length = 1 + age + temperature + age × temperature + age<sup>2</sup> + age<sup>2</sup> × temperature + age<sup>3</sup> + age<sup>3</sup> × temperature, with gamma distributed errors. The full quadratic model is similar, but lacks the cubic terms. *P* value refers to a  $\chi^2$  statistic for difference between the deviances of the full and reduced models. The terms listed under reduced models refer to terms sequentially removed from the full model.

**Table 2.** Hierarchical screening of terms for a forward-stepping empirical model of cod growth.

Terms	df	Change in deviance	<i>P</i> value
Null			
+ age	1	211.5	<0.001
+ temperature	1	66.4	<0.001
+ stock	6	82.0	<0.001
+ age + stock			
+ temperature	1	2.5	0.110
+ age × temperature	1	8.1	0.004
+ age + temperature			
+ stock	6	18.2	0.006
+ age × temperature	1	7.1	0.008
+ age + temperature + stock + age × temperature	1	6.9	0.009

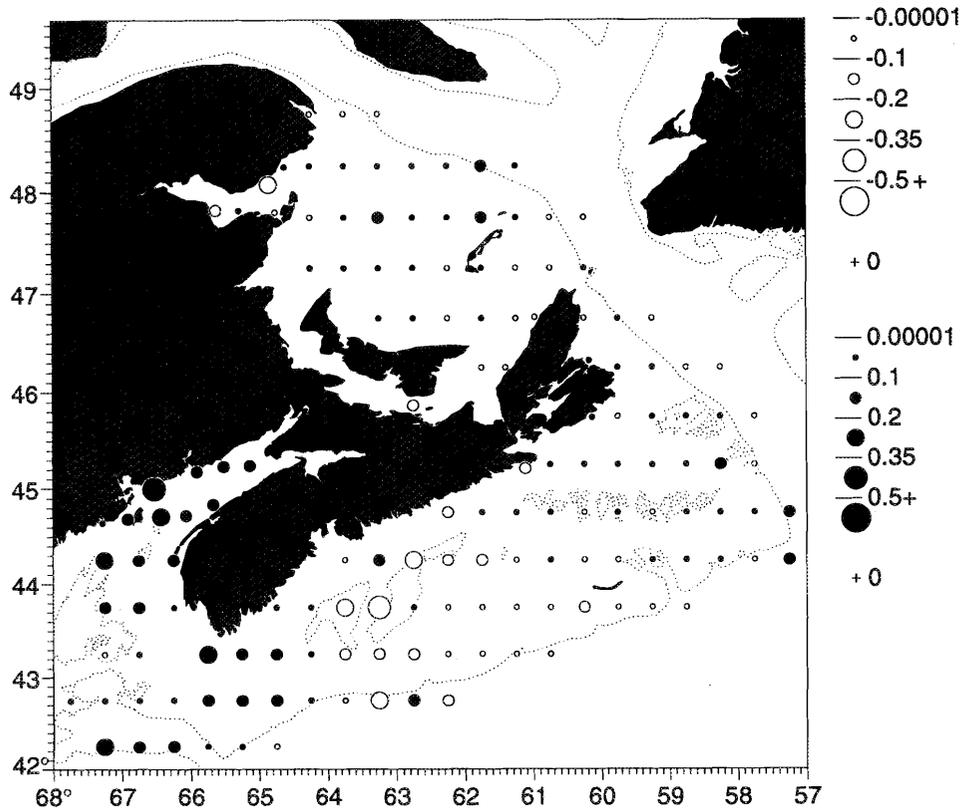
**Note:** The NAFO divisions corresponding to the stock term are as follows: 4T, 4Vn, 4Vs, 4W, 4X offshore banks, 4X Bay of Fundy, and 5Z.

All of the age-related residuals showed a similar geographic pattern, with relatively small residuals in the Gulf of St. Lawrence and Scotian Shelf, positive residuals in

the southern portion of the range, and negative residuals in the warm, deep basins of the Scotian Shelf. In other words, predicted lengths were smaller than observed in the south and larger than observed in the deep basins. Model fit elsewhere was relatively good. Spatial patterns in deviations from predicted values appeared to cross stock boundaries and thus were associated with regions rather than populations.

Using the temperature-parameterized growth model, we wished to answer the following question: could declining temperatures on the eastern Scotian Shelf have been responsible for the observed decline in length at age of cod in the region (Mohn and MacEachern 1994)? Bottom water temperatures (Fig. 10) and relative growth rates on the eastern Scotian Shelf have declined since the 1980s, whereas temperatures and relative growth rates further south have not. Using the observed lengths of age 2 cod as a starting point (smoothed with a 3-year running mean), we calculated annual growth increments for cohorts of cod from NAFO division 4Vs on the basis of observed 4Vs bottom water temperatures and the parameterized growth model. Note that these data were not identical to those used in fitting the model, since the latter used 5-year time blocks across the entire survey region, while the model predictions were based on annual temperatures in only 15% of the region. The predicted lengths of age 8 cod tended to reflect the

**Fig. 9.** Spatial distribution of the deviance residuals from the age- and temperature-based growth model for age 4 cod across all year blocks. In all age categories, fish length tended to be underestimated in the warm southern portion of the study area, and overestimated in the warm deep basins.



lengths that were actually observed, at least qualitatively (Fig. 11). In particular, the timing of the pre-1980 increase and the post-1980 decrease in length at age was well predicted by the model, although the rate of decline was underestimated. The fit of the model was not as good when fixed or predicted lengths at age 2 were used as starting points, suggesting that variations in growth during the first 2 years of life carried through to the adult stage. Temperature may also have played a role in the growth of cod less than 2 years old, since temperature and observed length at age 2 were significantly correlated ( $p < 0.05$ ).

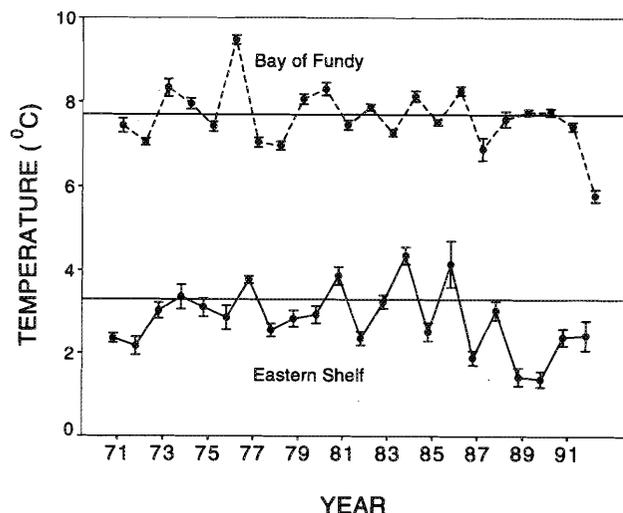
## Discussion

The large-scale spatial gradient in cod size at age along the eastern coast of Canada appears to be largely explicable on the basis of temperature alone. These results are consistent with previous growth studies on cod, in which a significant effect of temperature has been noted (Taylor 1958; Nakken and Raknes 1987; Loeng 1990; Jorgensen 1992; Brander 1995). This is not to say that temperature effects on fish growth are necessarily direct; various workers have reported that growth rate increased with temperature only in the presence of sufficient rations, presumably through the intermediary of increased consumption (Kohler 1964; Cui and Wootton 1988; Brown et al. 1989; Waiwood et al. 1991). While our analysis would not have

been able to differentiate between temperature and food effects if they were highly correlated in space, the documented importance of temperature on fish growth (Brett 1979; Ricker 1979; Houde 1989), in conjunction with the observed spatial gradient in temperature, suggests that food limitation alone was not responsible for the large-scale patterns in growth rate in the study area. Griffiths et al. (1992) noted that the growth in length of Arctic ciscoes (*Coregonus autumnalis*) was considerably more sensitive to temperature than was growth in weight; the latter was more strongly influenced by food availability and would probably be more apparent at smaller spatial and temporal scales.

The advantages of mapping patterns in fish growth are not restricted to ease of visualization (Brandt and Kirsch 1993). While the colour-coded contour maps certainly made it easier to see spatial patterns in relative size, it was the maps of the model residuals that highlighted the inadequacies of the growth model. Some discrepancy is unavoidable, because cod are not fixed particles in space. Indeed, cod from the Gulf of St. Lawrence migrate well outside the Gulf each winter, although growth during this period is relatively minor (Anonymous 1994). Seasonal temperature cycles also differ substantially among regions, suggesting that the length of the growing season is almost certainly dependent upon region. For example, bottom water temperatures in southwest Nova Scotia often stay

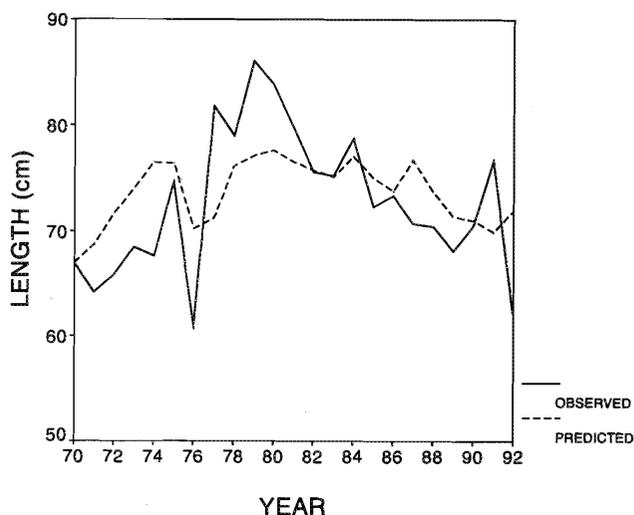
**Fig. 10.** Bottom water temperatures ( $^{\circ}\text{C}$ ) on the eastern Scotian Shelf and in the Bay of Fundy as recorded on RV surveys between 1971 and 1992. There have been no long-term shifts in temperature in the Bay of Fundy, but temperature has declined on the eastern Scotian Shelf since the mid-1980s.



above  $2^{\circ}\text{C}$  during the winter (Smith 1989), while much of the shallow water of the southern Gulf of St. Lawrence is below  $0^{\circ}\text{C}$  (Strain 1988). Thus, it is reasonable to expect a longer growing season in the southern portion of the range than in the northern portion, and hence growth underestimation (positive residuals) in the former. This effect was also apparent as a statistically significant stock effect in the growth model. Cumulative temperature within a year (akin to growing days) might be a more useful measure of growth temperature than is a point estimate of temperature during the summer. Presumably, there are regional variations in food availability that also affect the relative growth rate of cod. The negative residuals associated with the warm deep basins of the Scotian Shelf indicated the presence of undersized cod, pointing to the possibility of food limitation in those areas. Indeed, this model may be well suited to identifying regional variations in scope for growth (*sensu* Brandt and Kirsch 1993).

The age-temperature growth model presented here not only accounted for much of the observed variation in size at age in the waters off of eastern Canada, it provided reasonably accurate predictions of cod size at age in other regions. Jonsson (1965) reported mean August bottom water temperatures of 8.5, 6.7, 4.4, and  $3.6^{\circ}\text{C}$  in four hydrographic provinces off of Iceland, associated with age 6 cod of 81.2, 77.8, 68.7, and 65.0 cm, respectively. The predictions of the growth model lay within 7% of each of these values. Predictions of the length of age 4-6 cod in the Barents Sea were accurate to within 5% of observed values (Nakken and Raknes 1987), on the basis of the August bottom water temperatures of Loeng (1990). Similarly, the length of age 5 cod off the coast of Labrador (NAFO division 3K) was estimated to be 48.4 cm, versus an observed length of 50 cm (May et al. 1965). Finally, the length of age 5 West Greenland cod was estimated to within 3% of

**Fig. 11.** Observed and predicted lengths of age 8 cod (cm) on the eastern Scotian Shelf between 1971 and 1992. Model predictions were based on the parameters of Table 1 and observed age-specific bottom water temperatures in NAFO division 4Vs, using smoothed observed lengths at age 2 as starting points for the growth trajectories of each cohort.



observed values (Hermann and Hansen 1965), on the basis of July bottom water temperatures (Elizarov 1965). But despite the relative accuracy of these and other length at age predictions, the growth model is conceptually flawed. It is well known that growth rate is a function of not only environmental variables but fish size as well (Braaten 1984). In its current form, however, the model would predict that a shift in temperature would result in an annual increment that is a function of an age-temperature interaction rather than a size-temperature interaction. In other words, should a 4-year-old cod that had been reared at  $2^{\circ}\text{C}$  increase in length the same amount as a much larger 4-year-old cod that had been reared at  $8^{\circ}\text{C}$ , if the two were then placed in the same environment? On the basis of observations of growth trajectories in other species (Makinen and Ruohonen 1992), the answer would appear to be no, yet to our knowledge, all published linear growth models fail to make that prediction. Bioenergetic growth models should be able to avoid this problem, but face the additional constraints of obtaining measures of food availability and parameter estimates in wild fish.

Long-term shifts in water temperature appear almost certain to produce concomitant shifts in the growth rate of cod. More specifically, the decline in water temperature appears to explain at least some of the decline in size at age of eastern Scotian Shelf cod since the mid-1980s, with heavy exploitation of the faster growing fish possibly accounting for some of the remainder. Reduced water temperatures may also account for declines in the growth rate of cod in the Gulf of St. Lawrence and off Newfoundland. Similar reasoning has been invoked to explain long-term shifts in the relative size of cod elsewhere in the world (Nakken and Raknes 1987; Loeng 1990; Jorgensen 1992; Brander 1995). Thus, it seems odd that Frank et al. (1990)

referred only to growth effects owing to increased winter feeding as being among the global warming effects predicted to affect cod stocks. However, where stocks are near the limit of their range, it may be that temperature effects on growth will prove to be secondary to other factors, as has been reported for fish stocks on Georges Bank (Ross and Nelson 1992).

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