Comparison of size-at-age of larval Atlantic cod (*Gadus morhua*) from different populations based on size- and temperature-dependent growth models

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Abstract: This study presents the first intraspecific evaluation of larval growth performance across several different experimental scales, environments, and regions of a marine fish species. Size- and temperature-dependent growth models for larval and early juvenile Atlantic cod (*Gadus morhua*) are developed based on selected laboratory experiments with cod fed in excess. Observed sizes-at-age of cod from several experiments and stocks are compared with predictions from the models using initial size and ambient temperature history as inputs. Comparisons with results from other laboratory experiments reveal that the model predictions represent relatively high growth rates. Results from enclosure experiments under controlled seminatural conditions generally provide growth rates similar to those predicted from the models. The models therefore produce suitable reference growth predictions against which field-based growth estimates can be compared. These comparisons suggest that surviving cod larvae in the sea typically grow at rates close to their size- and temperature-dependent capacity. This suggests that climatic influences will strongly affect the year-to-year variations in growth of cod during their early life history owing to their markedly temperature-dependent growth potential.

Résumé : Cette étude présente la première évaluation intraspécifique de la performance de la croissance larvaire d'une espèce de poisson marin sur plusieurs échelles expérimentales différentes et dans divers environnements et régions. L'élaboration de modèles de croissance de larves et de très jeunes morues franches (*Gadus morhua*) en fonction de la taille et de la température se base sur des expériences en laboratoire choisies dans lesquelles les morues sont nourries en excès. Les tailles de la morue observées en fonction de l'âge dans plusieurs expériences et stocks sont alors comparées aux prédictions des modèles qui utilisent la taille initiale et la température ambiante expérimentée comme variables d'entrée. Des comparaisons avec les résultats d'autres expériences de laboratoire indiquent que les prédictions des modèles représentent des taux de croissance relativement élevés. Les résultats d'expériences en enclos dans des conditions contrôlées semi-naturelles fournissent généralement des taux de croissance semblables à ceux que prédisent les modèles. Les modèles fournissent donc des prédictions de référence adéquates de la croissance aux fins de comparaison avec les estimations de croissance déterminées en nature. Ces comparaisons indiquent que les larves de morue qui survivent dans la mer croissent généralement à des taux qui s'approchent de leur potentiel, compte tenu de leur taille et de la température. On peut donc croire que les influences climatiques affecteront fortement la variation d'une année à l'autre de la croissance des morues au début de leur cycle biologique à cause de leur potentiel de croissance fortement dépendant de la température.

[Traduit par la Rédaction]

Introduction

Fish larvae exhibit highly variable growth rates when raised at different temperatures and food levels (Houde 1989; Letcher and Bengtson 1993; Otterlei et al. 1999). Larval survival has also been shown to depend on food availability, where slow-growing and poorly conditioned larvae either directly or indirectly suffer elevated starvation-related mortality (Ellertsen et al. 1981; Werner and Blaxter 1981; Jonas and Wahl 1998). Growth and condition are closely linked in fish larvae and high priority is given to the allocation of energy to growth (Pedersen 1997; Finn et al. 2002). This may be a reflection of the high mortality associated with smaller sizes in the larval stage (McGurk 1986; Miller et al. 1988), where the advantage of growing faster (and bigger) outweighs the benefits of depositing energy storage for subsequent periods of food shortage. One of the consequences is that the time period from onset of food deprivation to starvation mortality does not increase noticeably with size in the larval stage (Miller et al. 1988; Jordaan and Brown 2003).

Size-at-age provides an integrated measure of the past feeding history and growth of surviving larvae. Specifically, smaller sizes-at-age than possible given the predicted capacity for growth at the prevailing environmental conditions indicate previous periods of food limitation that may have been associated with elevated mortality. A similar approach

Received 23 April 2004. Accepted 17 December 2004. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 20 May 2005.
J18084

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 doi: 10.1139/F05-008

has been applied in clinical medicine, where reference growth curves, indicating expected growth performances, are in common use to assess growth and development of infants (Onis et al. 1997; Victora et al. 2000). The problem of using size-at-age as a comparative measure in larval fish is that growth is strongly influenced by temperature conditions, making simple comparisons difficult (Øiestad 1984). Rather than a growth relationship in which size depends only on age as in homeotherms such as humans (Victora et al. 2000), ambient temperature must also be included in reference growth curves for fish. Temperature-corrected growth models for juvenile and adult fish have been used to compare growth rates of fish from different stocks (Brander 1995), but to date, no comprehensive comparisons of growth performance have been undertaken for the early life stages of a marine fish species. Here, I present a new approach to evaluate growth performance in young fish using Atlantic cod (*Gadus morhua*) as a model species.

Previously developed age-based growth models for cod larvae that are appropriate for constant temperature conditions (e.g., Campana and Hurley 1989; Otterlei et al. 1999) lack the flexibility needed when comparing offspring from variable temperature conditions. Therefore, the purpose of this study is firstly to provide general size-based models for growth in larval cod that incorporate temperature and initial size as input variables so that comparisons can be made across different experimental scales, environments, and regions. The models will then be compared with other laboratory studies to confirm that the model predictions are based on data from the highest laboratory growth rates available. Thereafter, the model will be validated against observation from enclosure studies under seminatural conditions that are characterized by high survival and growth rates (Øiestad 1984). Finally, the model outputs will be compared against growth estimates from the field obtained through otolith microstructure analysis. The growth performance of the larvae from the different environments is evaluated using a common metric, and the robustness of the model outputs is also investigated through evaluation of initial assumptions and temperature relationships. To my knowledge, this is the first attempt to evaluate the growth performance of surviving fish larvae from several field locations and environments relative to their size- and temperature-dependent growth potential. Based on the importance of size-dependent mortality in marine fish larvae (e.g., Miller et al. 1988; Bailey and Houde 1989; Houde 1997), it is hypothesized that surviving cod larvae at sea are generally characterized by relatively high growth rates.

Materials and methods

Model development

Size- and temperature-dependent growth (STDG) models are reparameterized from previously published Gompertz-type age- and temperature-dependent growth (ATDG) models (Otterlei et al. 1999). The models are based on data from extensive laboratory experiments with northeast Arctic (NA) cod and Norwegian coastal (NC) cod conducted over two seasons. The cod larvae were fed natural plankton in excess at constant temperatures in the range 4–14 °C under a daily and seasonally fluctuating light cycle. Larvae were sampled weekly over a 2-month period each year and measured for length and weight (range approximately 0.02–200 mg dry weight (DW) and 3.5–45 mm live standard length (SL)). The lower temperature groups did not cover the same size range, and the model is therefore not adequately documented outside the size range of 0.03–50 mg DW for the entire temperature range. The original ATDG models indicated an asymmetric dome-shaped relationship between age and growth rate at the given temperatures, and the models explained more than 95% of the variability in size-at-age (see Otterlei et al. (1999) for further details). In this study, third-degree polynomial models are thus selected as the basis for the STDG models to accommodate for this initial increase and subsequent relatively slower decline in growth rate with increasing fish size. The daily specific growth rate (SGR) (percent per day) is given as

$$(1) \qquad \mathrm{SGR} = c_0 + c_1 \ln\mathrm{DW} + c_2 (\ln\mathrm{DW})^2 + c_3 (\ln\mathrm{DW})^3$$

with $c_i = a_i + b_i\mathrm{Temp}$, where Temp is the average daily temperature (°C) and ln DW is the natural log of the estimated stock-specific larval dry weight (mg) on a given day. A quadratic temperature term is not used, since a previous study has shown that the temperature effect on growth was approximately linear in the temperature range of the original data (Otterlei et al. 1999).

The parameters of the models are estimated by stepwise nonlinear procedures (StatSoft Inc. 1995) using the daily temperature-specific growth rates and dry weights from the ATDG models as inputs (Otterlei et al. 1999). Nonsignificant terms of eq. 1 were excluded in the final models. In this paper, specific growth rate is defined as

$$(2) \qquad \mathrm{SGR} = 100 - (e^{g} - 1)$$

where g is the instantaneous growth coefficient either obtained by derivation of the Gompertz size-at-age function (Otterlei et al. 1999) or defined as

$$(3) \qquad g = (\ln\mathrm{DW}_2 - \ln\mathrm{DW}_1)/(t_2 - t_1)$$

where DW_i is the dry weight at time t_i. Separate models are fitted to the data for NA cod and NC cod, and only significant parameters are included in the final models.

Data selection

The following criteria were applied when selecting data sets to be included in the comparative analysis: (*i*) the larval groups were not fed restricted diets and the fish exhibited significant positive growth (only data from highest food levels were used from laboratory and enclosure studies), (*ii*) the data were available from personal sources and (or) published in peer-reviewed journals, (*iii*) the durations of the experiments were beyond 3 weeks and beyond period of initial starvation mortality, (*iv*) initial and (or) final sizes were available, including information on shrinkage correction, (*v*) at least two measurements of size-at-age (or an alternative model output) from the same population were available (single cross-sectional data were used on two occasions for field studies), (*vi*) data where both the larval sizes and temperatures were outside the main range of the model domain at any given time were not included (cases where either the temperature exceeded the 4–14 °C range or the larval size exceeded the 0.03–50 mg DW range are mentioned explic-

itly), (*vii*) temperature data were presented in the paper or could be approximated from other sources (e.g., internet, see below), and (*viii*) the larval groups had only been feeding on live plankton. These criteria were chosen to select good-quality data from well-growing known-aged laboratory and enclosure groups as well as aged groups from the field. It was not the intention of this study to present a complete review of all published experimental growth results of larval cod; rather, the intention was to select those studies that a priori could be expected to contain growth rates that best described the growth potential. Two model predictions are also included using the original data underlying the ATDG and STDG models, the 6 and 10 °C NC cod data, which represent the series with the poorest and best fit to the original ATDG models, respectively (Otterlei et al. 1999). In total, 40 data series from 25 studies are included in this study (Table 1).

Data analysis

The models were initialized with the average initial sizes-at-age as inputs. In cases where several replicate units were used in the experiment, the average of the replicates was used. Since the STDG models like the ATDG models produce monotonically increasing sizes, the initial growth rates were taken to represent the embryonic growth (Otterlei et al. 1999). To correct for variable amounts of yolk included in the published initial dry weights, I used the following approximation to relate early embryonic weight to total larval weight (including yolk) based on data from cod larvae kept at 7 °C (Solberg and Tilseth 1987):

$$\text{EDW} = \text{TDW}(0.7 + 0.05\text{DPH}) \quad (4)$$

where EDW is embryo dry weight, TDW is total dry weight including yolk, and DPH is days posthatching. For larvae older than 6 days, the EDW is set equal to the total dry weight (termed DW hereafter). If daily temperature estimates were not available, linear interpolations between days were used to obtain the data for the models. If depth-stratified temperature data were available, the distribution of larvae in the water column determined whether the mean water temperature of the water column or the temperatures at specific depths (maximum temperatures) were used. The models were run with temperatures ranging from 2 to 16 °C, slightly outside the range of 4–14 °C from which the model was developed (Table 1). The model was also run for sizes exceeding the 50 mg DW as long as the temperature at this point was between 8 and 14 °C (see above). When the average initial weights are unknown, i.e., for field data, an initial DW of 45 μg was used (corresponding to 4.4 mm live SL). No correction for shrinkage was used when the same fixation had been used throughout a study. The model predictions were calculated throughout the period of investigation on a daily basis with the daily temperature history and estimated size each day as inputs. All of the laboratory and mesocosm studies are based on known-age material, while the field material has been aged by use of otolith microstructure analysis (Campana 1992). Average estimated ages of larvae from the different data series are used to estimate mean hatch dates and corresponding temperature histories.

No size-dependent mortality corrections were applied to any of the data sets. Typically, the apparent growth rates of a cohort are overestimates of individual growth rates when smaller individuals in a cohort of larvae have relatively higher mortality (Folkvord 1997). In papers where lengths were reported as the size measure instead of DW, I used the following length to weight relationships when no other relationship was presented in the paper:

$$\ln \text{DW} = -9.38 + 4.55 \ln \text{SL} - 0.2046 (\log \text{SL})^2 \quad (5)$$

$$\ln \text{SL} = 2.296 + 0.277 \ln \text{DW} - 0.005128 (\log \text{DW})^2 \quad (6)$$

where SL is live standard length (mm) and DW is dry weight (mg) from frozen specimens (data from Folkvord et al. 1999; $n = 509$, $r^2 = 0.995$, SE of the estimate = 0.130 and 0.035, respectively). Total length was estimated from SL with the relationship

$$\text{TL} = -0.20 + 1.082\text{SL} \quad (7)$$

where TL is live total length (mm) (R.N. Finn, Department of Biology, University of Bergen, N-5020 Bergen, Norway, unpublished data).

Separate STDG models are used for offspring of NA cod and NC cod. For the other laboratory studies with offspring from other populations, I compare their growth rates against the NC cod model outputs, since this is the model that predicts the highest growth rates. The sizes-at-age are estimated for the duration of the experiments or to a maximum of 90 DPH. The model outputs are compared directly with the observed size-at-age for the included studies. In addition, I calculate the growth performance in the different studies relative to model predictions as

$$\text{Growth ratio} = \text{average observed SGR} / \text{average modeled SGR} \quad (8)$$

where common initial weights and respective final weights are used. The growth ratio thus represents the average proportional daily growth rate of the observed versus modeled growth rates. The same growth performance measure was used when comparing the effects of changing the initial size or the subsequent temperature history. In this case, the modified growth rate was divided by the original growth rate.

To evaluate the effect of initial size on the size predictions of the field data, three initial sizes (30, 45, and 67.5 μg) were used in a 70-day, 6 °C simulation. These weights were termed lower, middle, and upper initial size estimates, and the relative initial size ratio was 1.5 between middle and lower and upper and middle. In addition, I ran a test of the temperature sensitivity by adding 1 °C to or subtracting 1 °C from the estimated temperature for Georges Bank from Campana and Hurley (1989) throughout the 90-day period. In both cases, the effect of the parameter change was estimated by relative difference in final weights and the change in growth ratio.

Results

STDG models

For both the NC and NA data series, a five-parameter STDG model explained nearly all of the variability of the estimated growth rates of the ATDG models (Otterlei et al. 1999) (stepwise nonlinear estimation, $r^2 > 0.997$, $n = 434$ and 451 for NC cod and NA cod, respectively). The models predict a maximum growth rate prior to initiation of metamorphosis (at around 0.7 mg DW and 9 mm SL) and a linear

Table 1. Sources of growth- and size-at-age data of larval and juvenile cod (*Gadus morhua*) used in the study.

Reference	Study code	Area or place of study	Temperature (°C)	Initial DW used (μg)	Duration (days)	Fixation and measures	Comments (temperature data from paper unless specified otherwise)
Laboratory studies							
Laurence 1978	L1	Rhode Island, USA	4, 7, 10	36–43 on day 0	35–49	Not specified	First pioneering laboratory growth study on larval cod
Laurence et al. 1981	L2	Rhode Island, USA	7	44 on day 0	42	Fixed in formalin	Low survival in highest prey density group (sampled to extinction)
Buckley et al. 1993	L3	Rhode Island, USA	7[a]	35 on day 0	42	Fresh for SL, frozen for DW	31%–44% survival in high prey density group
Otterlei et al. 1999	L4	Bergen, Norway	6, 10 (4, 8, 12, 14 not shown here)	30 on day 0	56	Fresh for SL, frozen for DW	5%–45% survival, basis for growth models, otoliths removed before DW measurements, only NC cod data shown here
Folkvord et al. 1999	L5	Bergen, Norway	8	38 on day 0	56	Fresh for SL, frozen for DW	47%–65% survival of NA cod, six replicates, used SL–DW relationship from this study
Baskerville-Bridges and Kling 2000	L6	Maine, USA	10–11, experiment I	30 on day 0	44	Fresh for SL, frozen for DW	Fed rotifers and *Artemia* (from day 22 or 16), 29%–36% survival (experiments I and II in paper)
			7–8, experiment II		36		
Puvanendran and Brown 2002	L7	Newfoundland, Canada	8	48 on day 0	42	Fresh for SL and DW	High light intensity and 24:0 light cycle gave best growth, 30%–40% survival
Mesocosm studies							
Ellertsen et al. 1981	E1	Flødevigen, Norway	4.5–9.9	50 on day 11	52	4% buffered formaldehyde	First group 1976, first mesocosm study of NC larval cod growth in a century, 10% survival
Pedersen et al. 1989	E2	Tromsø, Norway	2.0–11.5 (max. temperature)	34 on day 4	50	4% buffered formaldehyde	Low initial temperatures in 1987, 7% survival, several releases[b]
Olsen et al. 1991	E3	Tromsø, Norway	6.1–14.7 (mean temperature)	75 on day 11	70	4% buffered formaldehyde	Rapid growth in 1989, larval DW estimated from SL[b]
Blom et al. 1991	E4	Øygarden, Norway	3.7–11.9 (mean temperature)	61 on day 6	80	4% buffered formaldehyde	1988 NC cod data, last samples taken with dip net, 23% survival to metamorphosis
Blom et al. 1994	E5	Øygarden, Norway	5.8–9.8	32 on day 2	45	4% buffered formaldehyde	Average of two strains of NC cod in 1991, 23% survival[c]
Folkvord et al. 1994	E6	Austevoll, Norway	6.8–11.2 (max. temperature)	33 and 34 on day 4 and day 5	40, 29	4% buffered formaldehyde	1985 cohorts 1 and 2 with NC cod, 40% and 15% survival
van der Meeren et al. 1994	E7	Austevoll, Norway	4.4–12.2, 7.4–12.3	44 and 42, 42 and 40 on day 2	48, 36	Fresh for WW and DW	1993 data (experiments I and II) on NC and NA cod, 28%–83% survival

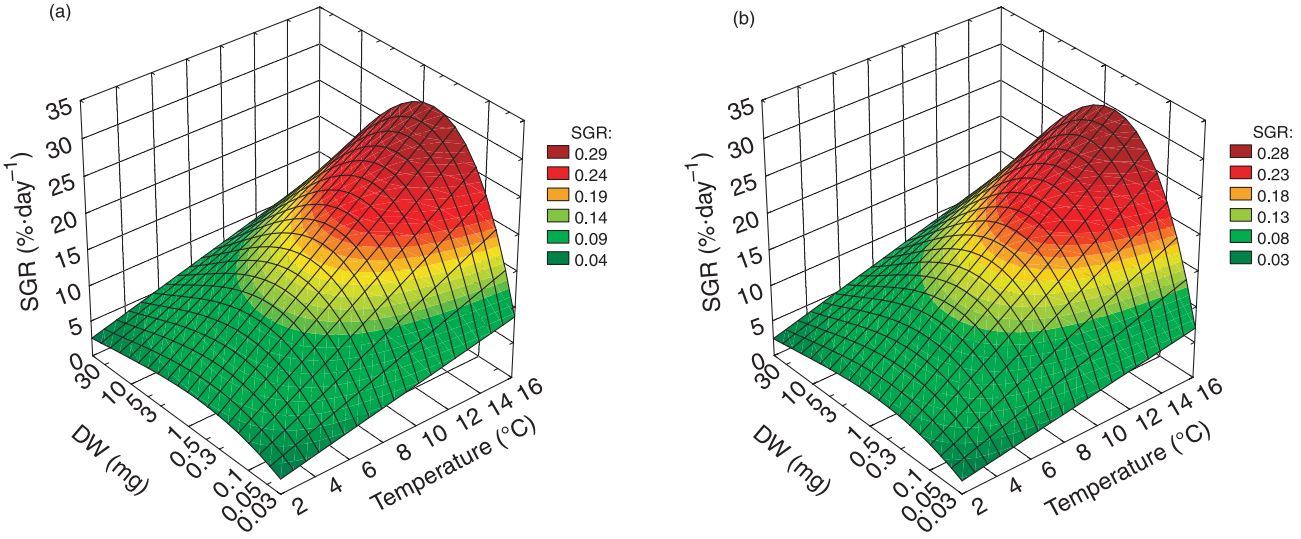
Table 1 (*concluded*).

Reference	Study code	Area or place of study	Temperature (°C)	Initial DW used (μg)	Duration (days)	Fixation and measures	Comments (temperature data from paper unless specified otherwise)
Field studies							
Bolz and Lough 1988	F1	Georges Bank, Northwest Atlantic	4.6–10.2	45 on day 0	90	Corrected for shrinkage	Temperature data from Campana and Hurley (1989), sampling with 61-cm Bongo net and 1- to 10-m MOCNESS and an otter trawl for larger cod
Campana and Hurley 1989	F2	Browns and Georges banks, Northwest Atlantic	5.3–8.4, 5.1–9.9	45 on day 0	120 (90 used)	Not corrected for shrinkage	First age- and temperatue-dependent growth model for field larvae, 3 mm TL at day 0, sampling with 61-cm Bongo net
Meekan and Fortier 1996	F3	Scotian Shelf, Northwest Atlantic	7.6–2.3, 8.0–3.1	45 on day 0	80	Fresh for SL	Temperature data from Department of Fisheries and Oceans, S1 and S2 cohorts, sampling with 2-m^2 trawls
Suthers and Sundby 1996	F4	Browns Bank and northern Norway, Northeast Atlantic	2.5–6.0, 5.9–8.7	45 on day 0	90, 80	Not corrected for shrinkage	Data from both sides of the Atlantic, temperature data for Browns Bank from Department of Fisheries and Oceans and for Northeast Atlantic from Sundby (2000), sampling with 5- and 10-m^2 midwater trawls, respectively
Begg and Marteinsdottir 2000	F5	Northwest Iceland, North Atlantic	7.5–10.6, 3.0–8.2	45 on day 0	93, 84	Modeled fresh TL	Data from 1988, northern and southern area, used 57.5 and 45 mm as reported final TL, sampling with a 324-m^2 pelagic trawl
Anderson and Dalley 2000	F6	Grand Banks, Northwest Atlantic	3.7–7.8, 5.5–8.8	45 on day 0	65, 68	Fresh for TL	Data from cold year (1997) and warm year (1996), authors used 3.5 mm TL on day 0, sampling with 61-cm Bongo net and 73-m^2 IYGPT trawl

Note: L, E, and F denote laboratory, enclosure, and field studies, respectively. NA, northeast Arctic cod; NC, Norwegian coastal cod. Initial weights have been corrected for presence of yolk. SL, standard length; DW, dry weight; WW, wet weight; TL, total length.

[a]L. Buckley, University of Rhode Island/National Oceanic and Atmospheric Administration (URI/NOAA) Cooperative Marine Education and Research Program, Graduate School of Oceanography, Narragansett, RI 02882, USA.
[b]T. Pedersen, Norwegian College of Fisheries Science, University of Tromsø, 9001 Tromsø, Norway.
[c]G. Blom, Department of Biology, University of Bergen, N-5020 Bergen, Norway.

Fig. 1. Plots of size- and temperature-dependent growth models for (*a*) Norwegian coastal (NC) Atlantic cod (*Gadus morhua*) and (*b*) northeast Arctic (NA) cod. Equation for each relationship: NC cod, specific growth rate (SGR) = 1.20 + 1.80·temperature – 0.078·temperature·ln DW – 0.0946·temperature·(ln DW)^2 + 0.0105·temperature·(ln DW)^3; NA cod, SGR = 1.08 + 1.79·temperature – 0.074·temperature·ln DW – 0.0965·temperature·(ln DW)^2 + 0.0112·temperature·(ln DW)^3. DW, dry weight.



increase in growth rate with temperature at any given size within the model domain (Fig. 1). At the upper size range, minimum predicted growth rates were found at 450 and 600 mg DW (55–59 mm SL) for the NA cod and NC cod, respectively. Beyond these sizes, the predicted growth rates slowly started to increase again. This is unrealistic, and the models should therefore not under any circumstance be used beyond the size of minimum growth rate. At 0 °C, the models predict size-independent growth rates slightly above 1%·day^{-1}, but further experimentation is needed at low temperatures to verify if this is realistic. At the high end of the temperature spectrum, the growth will eventually cease when temperature approaches lethality for cod (approximately 16 °C for newly hatched larvae (Iversen and Danielssen 1984) and above 20 °C for early juveniles (Otterlei 2000)), while the STDG models will still predict linearly increasing growth rates with increasing temperature. The models should thus be used with caution at temperatures below 4 °C and above 14 °C for which data were available to parameterize the STDG models, although maximum growth of early cod juveniles has been observed at 16–18 °C (Otterlei 2000). The estimated daiy NC cod growth rates were typically between 0.2% and 0.5% higher than the NA cod growth estimates within the data range used. Overall, the STDG models were considered to be suitable alternative parameterizations of the original ATDG models, since they were easier to implement in situations with changing temperature. In the ADTG models, a new age-at-size has to be calculated every time the temperature changes to reflect the age that the larvae should have as if it had been growing at the same temperature throughout. Otherwise, the larvae will have the "wrong" size according to the current age and temperature to be used in the ATDG model. The STDG models are used in the remainder of this study.

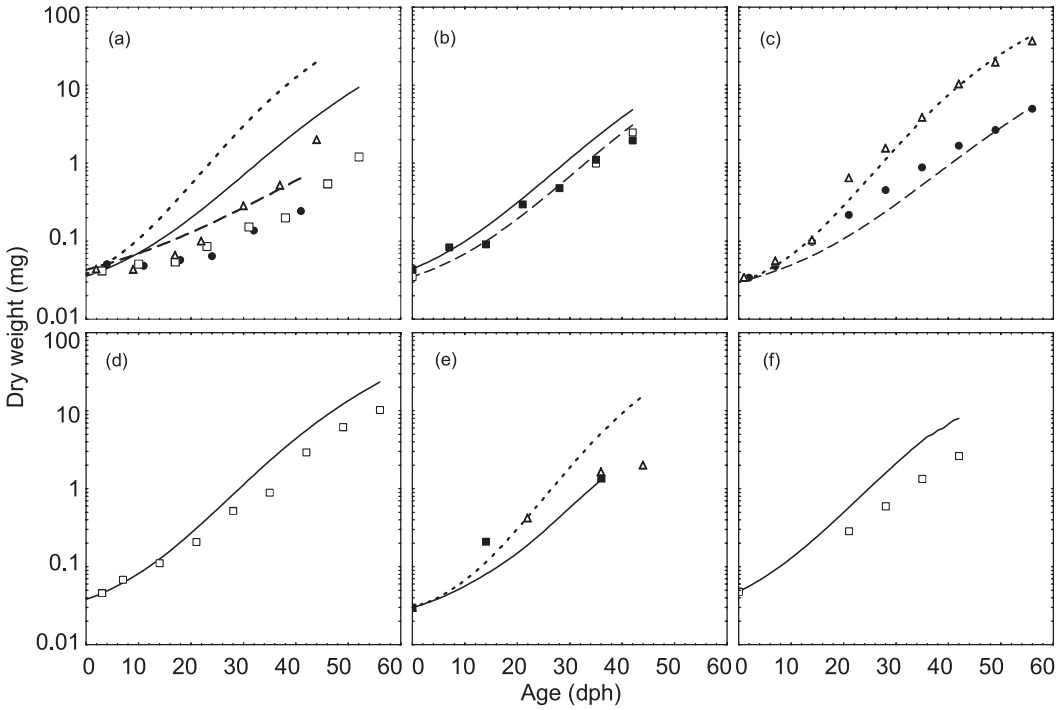
Comparative analyses of laboratory studies

The STDG models often predicted larger sizes than the observed sizes-at-age in the laboratory studies. This was especially true for the oldest study included in the analysis (Laurence 1978) (Fig. 2*a*). In this study, the final size-at-age predicted by the STDG model was up to 10 times higher than the observed size-at-age. Subsequent experiments in the same laboratory showed a much closer correspondence between predicted and observed size-at-age (Laurence et al. 1981; Buckley et al. 1993) (Fig. 2*b*). Strong correlations were also found between the model and the original data underlying the model for NC cod at 10 °C (best series fit), while the model initially underestimated the growth somewhat for NC cod at 6 °C, the poorest fit of the original data series (Otterlei et al. 1999) (Fig. 2*c*). Subsequent studies from the same laboratory (Folkvord et al. 1999) (Fig. 2*d*) and other laboratories (Baskerville-Bridges and Kling 2000; Puvanendran and Brown 2002) (Figs. 2*e* and 2*f*), on the other hand, indicate that the model predictions are representing relatively high larval cod growth rates. In the first experiment by Baskerville-Bridges and Kling (2000), a reduction in observed growth relative to the model in the latter half of the experiment coincides with the transition in feeding from rotifers to *Artemia*.

Validation of growth potential in enclosure studies

Observed growth rates from the enclosure studies were in general in agreement with the high predicted growth rates from the STDG models (Fig. 3). The first mesocosm study carried out in Flødevigen, Norway, in the mid-1970s was no exception (Ellertsen et al. 1981), although relatively higher growth rates were obtained in the same mesocosm in a later study (Clemmesen et al. 2003) (Figs. 3*a* and 3*i*). Subsequent experiments in larger enclosures (macrocosms) confirmed the good agreement between the NC cod STDG model and observed growth patterns (Blom et al. 1991, 1994; Folkvord et al. 1994) (Figs. 3*c* and 3*d*). In the study by Folkvord et al. (1994), the highest growth rates were observed and predicted for the second cohort released 10 days after the first cohort at somewhat elevated ambient temperatures due to the spring season temperature increase. Up to 10-fold differences in

Fig. 2. Observed (points) and predicted (lines) sizes-at-age (dph, days posthatch) from different laboratory studies. Within each panel, the dotted line and triangles represent the higher average temperature series, the solid line and squares the midtemperature series, and the dashed line and circles the lower average temperature series. Data from (*a*) L1, (*b*) L2 (solid line) and L3 (dashed line), (*c*) L4 (10 °C (dotted line) and 6 °C (dashed line)), (*d*) L5, (*e*) L6 (experiment I (dotted line) and experiment II (solid line)), and (*f*) L7.



size-at-age were observed between years in one of the mesocosms in northern Norway (Pedersen et al. 1989; Olsen et al. 1991), but according to the STDG model, this was mainly attributable to the differences in ambient temperature between years (Fig. 3*b*). Experiments in bag enclosures generally yielded very similar model predictions compared with observed final sizes (Suthers et al. 1999; van der Meeren and Jørstad 2001; van der Meeren and Moksness 2003) (Figs. 3*f*–3*h*), although the observed growth in the study by Finn et al. (2002) was somewhat slower initially than predicted. On the other hand, higher than expected growth rates were observed for NC cod in the study by van der Meeren et al. (1994), where offspring were over twice as heavy as predicted at the end of the experiment in both series studied (Fig. 3*e*). The same was the case for offspring of NA cod simultaneously reared in the same enclosures (data not shown). Overall results from the enclosure studies generally confirmed an acceptable accuracy of the size-at-age predictions of the STDG models, indicating that they provided useful representations of the growth potential in larval cod.

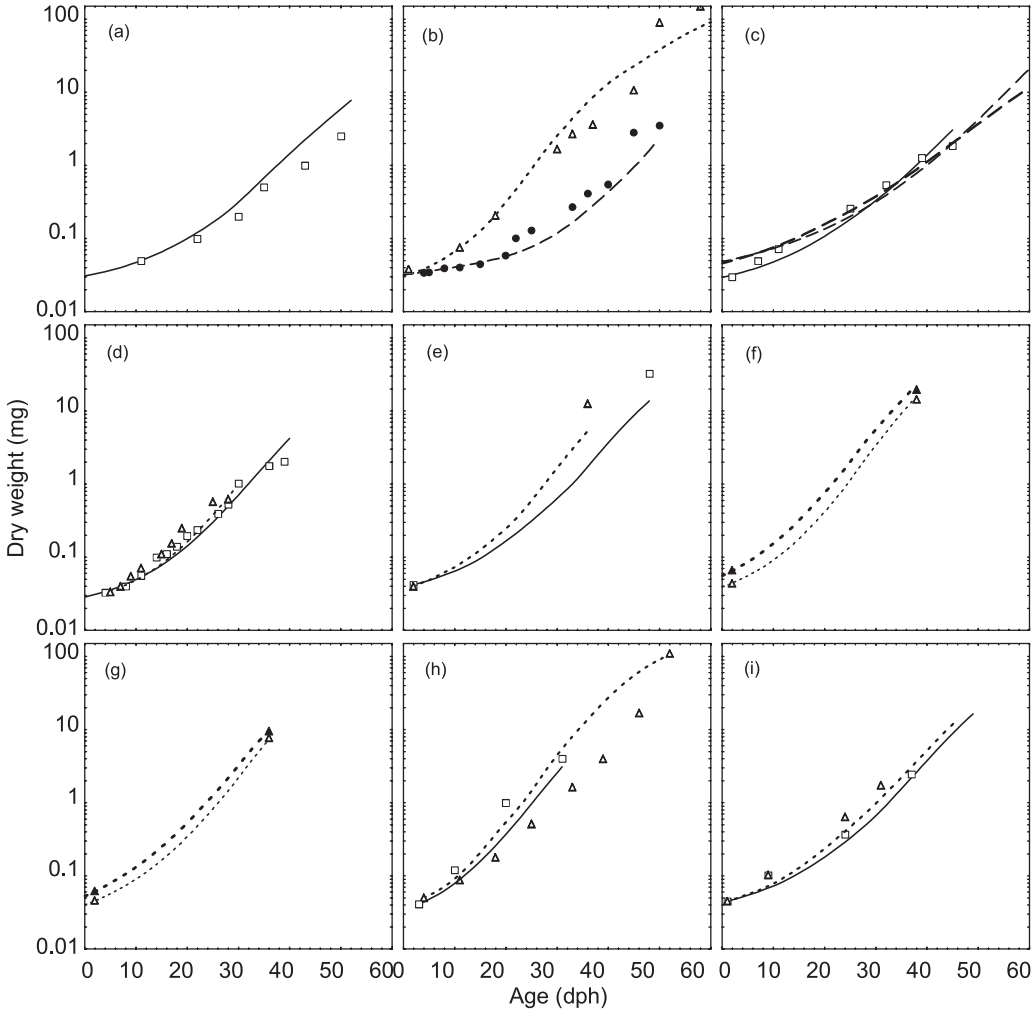
Growth performance of cod larvae at sea

The STDG model predicted a somewhat slower initial growth than reported by Bolz and Lough (1988) in their study of fish from the Georges Bank (Fig. 4*a*). Observed and predicted size-at-age converged as the fish became larger, however. In contrast, the predictions from the Campana and Hurley (1989) model, using the same temperature field, were relatively similar initially when taking into account that they had not corrected the larval lengths for shrinkage and that the model was initialized with a TL at hatching of 3 mm (Fig. 4*a*). However, for older cod larvae, an increasing discrepancy is noted between the predictions from the Campana and Hurley (1989) model and the STDG and Bolz and Lough (1988) model predictions (Fig. 4*a*). This is largely due to a low predicted growth from the Campana and Hurley (1989) model in older larvae at relatively higher temperatures in the latter part of the study (Figs. 4*a* and 4*b*). The Campana and Hurley (1989) model has a temperature optimum at 5.9 °C, and at 4 °C, the growth pattern of the Campana and Hurley (1989) model is initially similar to that predicted from the STDG model (Fig. 4*b*). However, at a constant temperature of 9 °C, the models produce clearly divergent results (Fig. 4*b*).

Meekan and Fortier (1996) presented data from late autumn – early winter spawning cod, which, in contrast with the other cod in this review, experienced a significant temperature decrease during their early life history. There were no temperature series presented in the paper, but using the data from a hydrographical station in the area (data source: Department of Fisheries and Oceans Canada, average of 20 and 30 m at subarea 11, Emerald Bank; http://www.mar.dfo-mpo.gc.ca/science/ocean/tsdata.html), the two surviving cohorts show a size-at-age close to the predicted sizes (Fig. 4*c*). The cohort with the largest size-at-age (1992–1993) came from the warmest of the two years in the study, which was about 1 °C warmer during the first 2 months of the larval period (Meekan and Fortier 1996).

Growth data from both the eastern and western Atlantic were presented by Suthers and Sundby (1996). Although the day length differences experienced off the Canadian and Norwegian coasts may favor growth of cod from the latter region, the ambient temperature differences in the two regions seem to be the main factor explaining the observed differences in growth (Fig. 4*d*). In both cases, the

Fig. 3. Observed (points) and predicted (lines) sizes-at-age (dph, days posthatch) from different enclosure studies. Within each panel, the dotted line and triangles represent the higher average temperature series, the solid line and squares the midtemperature series, and the dashed line and circles the lower average temperature series. Thicker lines of same type in the same panel indicate size- and temperature-dependent growth predictions versus model predictions from the source paper (regular thickness) and solid symbols represent heavier initial weights. Data from (*a*) E1, (*b*) E2 (dashed line) and E3 (dotted line), (*c*) E4 (dashed lines) and E5 (solid line), (*d*) E6 (cohort 1 (solid line) and cohort 2 (dotted line)), (*e*) E7 (experiment I (solid line) and experiment II (dotted line)) (only Norwegian coastal (NC) Atlantic cod (*Gadus morhua*) data shown), (*f*) E8 (NC cod (dotted line) and northeast Arctic (NA) cod (thick dotted line)), (*g*) E9 (NC cod (dotted line) and NA cod (thick dotted line)), (*h*) E10 (dotted line) and E12 (solid line), and (*i*) E11 (mesocosm 1 (solid line) and mesocosm 2 (dotted line)).

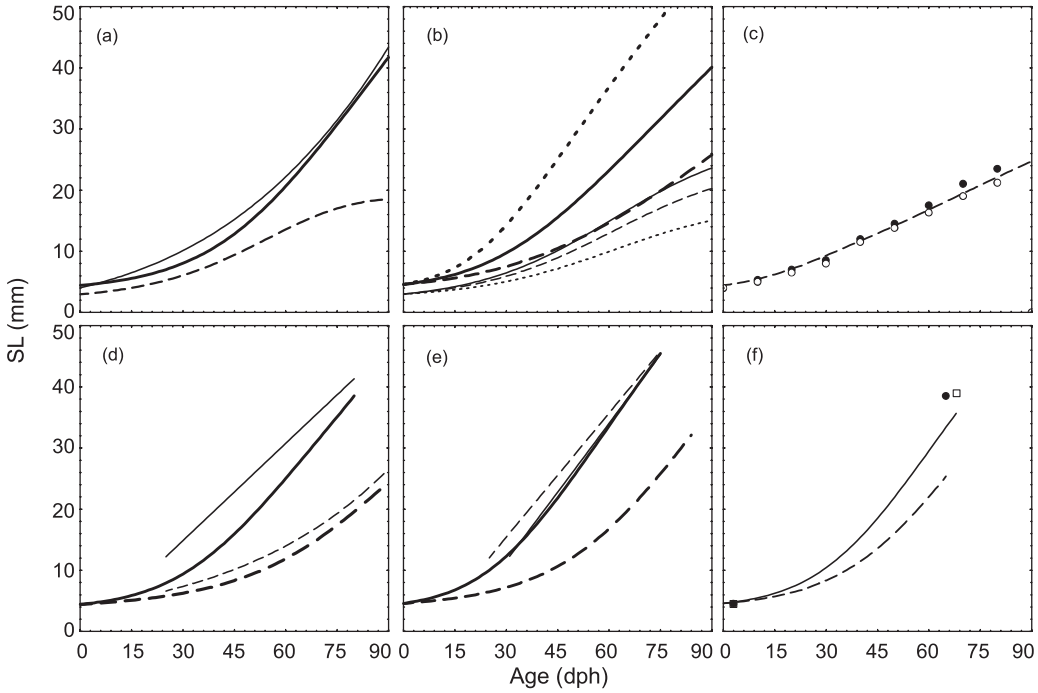


observed sizes-at-age were higher than predicted based on the STDG models (Fig. 4*d*). The same was also the case for the selected data from Begg and Marteinsdottir (2000) off the coast of Iceland. A good agreement was evident using the data from the southern (and warmer) part of the coast, while the cod from the northern (and colder) regions had apparently been growing much better than expected (Fig. 4*e*). This discrepancy was also present using the data from a cold year (1997) and a warm year (1996) off Newfoundland (Anderson and Dalley 2000). Again, a relatively good agreement was seen between observed and predicted size in the warm year, while the fish from the cold year seemed to have been growing much better than expected (Fig. 4*f*).

Comparison of growth performance of cod from different spatial scales

When comparing the growth performance in the various studies conducted at different scales, it is clear that the STDG models are based on some of the best-performing laboratory groups in the literature (Fig. 5*a*). The data of the larval groups from Laurence (1978), which have been used in several modeling studies, appear as the poor-performing outliers in this case, obtaining less than 70% of the average daily growth rate of the better performing groups. The best growth performance was found in the recent paper by Baskerville-Bridges and Kling (2000) (experiment II), which had marginally better average growth rate than expected (growth ratio of 1.01). Higher growth ratios are seen in the enclosure data series, which generally confirm the high growth rates experienced in these systems (Fig. 5*b*). In addition, the survival rates from some of these enclosure studies are among the highest reported for cod larvae in the literature (Table 1). Summarizing the results from the field investigations, it becomes clear that the surviving larvae in general

Fig. 4. Observed (points) and predicted (lines) sizes-at-age (dph, days posthatch) from different field studies. Within each panel, the dotted line represents the higher average temperature series, the solid line the midtemperature series, and the dashed line and circles the lower average temperature series. Thicker lines of same type in the same panel indicate size- and temperature-dependent growth model predictions versus model predictions from the source paper (regular thickness). Data from (*a*) F1 (solid line) and F2 (dashed line), (*b*) F2 (9 °C (dotted line), 6 °C (solid line), and 4 °C (dashed line)), (*c*) F3 (warmer 1992–1993 season (solid circles) and colder 1991–1992 season (open circles)), (*d*) F4 (Norwegian coast (solid line) and Canadian coast (dashed line)), (*e*) F5 (southern Iceland (solid line) and northern Iceland (dashed line)), and (*f*) F6 (warmer 1996 season (solid line) and colder 1997 season (dashed line)). SL, standard length.



have been growing at rates close to their estimated potential (Fig. 5*c*). The only exception seems to be the output from the Campana and Hurley (1989) model, which clearly predicts a lower average growth than reported from the original data (Bolz and Lough 1988). The two instances of very high growth rates in the field are both based on data from cod stocks in cold-water environments (see below).

Effects of changes in initial size and temperature on subsequent growth

In the field studies, the initial sizes of the fish were generally unknown. The start weight was therefore set to 45 μg, which is somewhat above average for the laboratory and enclosure studies (Table 1). A preliminary sensitivity analysis was undertaken to evaluate the effects of changing the initial weights. Permitting 50% initial weight differences (45 versus 30 μg, middle versus lower, and 67.5 versus 45 μg, upper versus middle) generated weight differences of 100%–150% after 30–40 days. The difference in sizes increased initially due to the increasing growth rate with size for smaller larvae and then declined after the size of maximum growth had been attained (Fig. 6). In the example with cod growing at 6 °C, the size differences were reduced back close to the original size difference within a 70-day period (largest group being 50%–80% heavier). The corresponding growth ratios were 1.00 (upper/middle) and 1.05 (middle/lower) when using the respective initial weights and 1.06 and 1.12 when a using a common (and incorrect) initial weight. Thus, a 50% error in the initial weight estimate would only generate a growth ratio difference of about 0.06 when calculated over a 70-day period. Running the same simulation at higher temperatures tended to increase the initial size difference at a younger age but diminished the subsequent differences between the groups more rapidly as well.

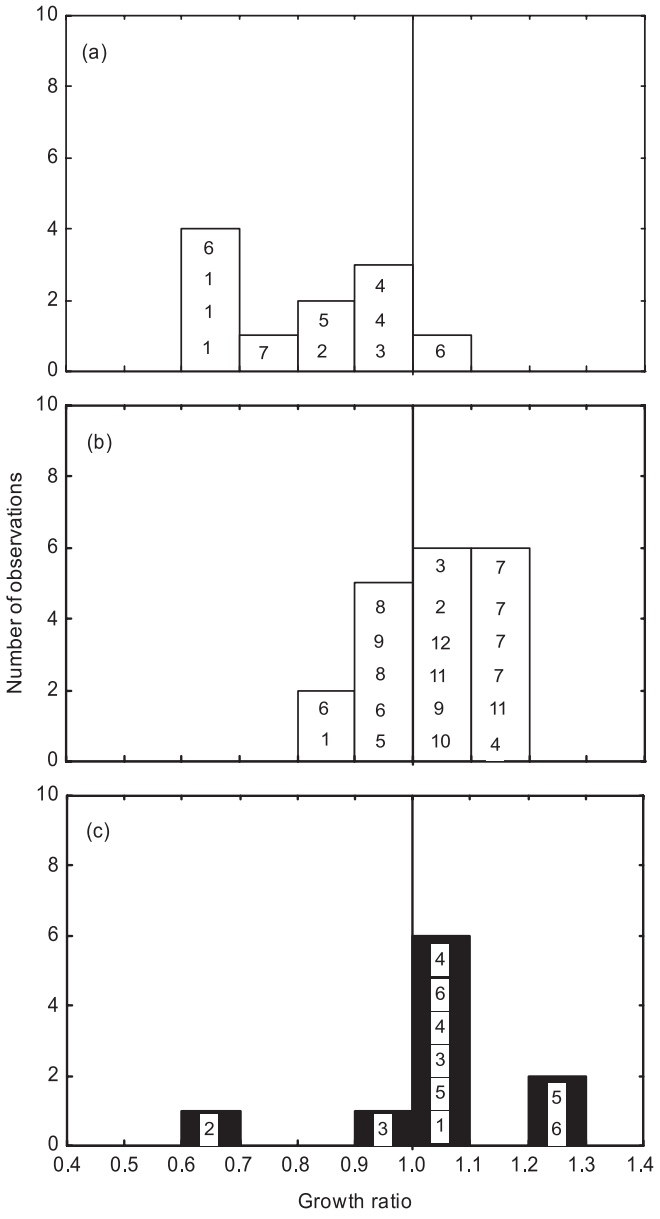
The effects of under- or overestimating the temperature history were simulated by altering the temperature for Georges Bank by 1 °C up or down. A 1 °C elevation throughout the study period increased the final weight by 50%, while a 1 °C reduction throughout the growth period led to a 40% reduction in final weight compared with the original predictions. The corresponding growth ratios changed from 1.02 to 0.97 and 1.10, respectively, approximately the same effect on the growth ratio as reported for the change in initial size.

Discussion

STDG model justification

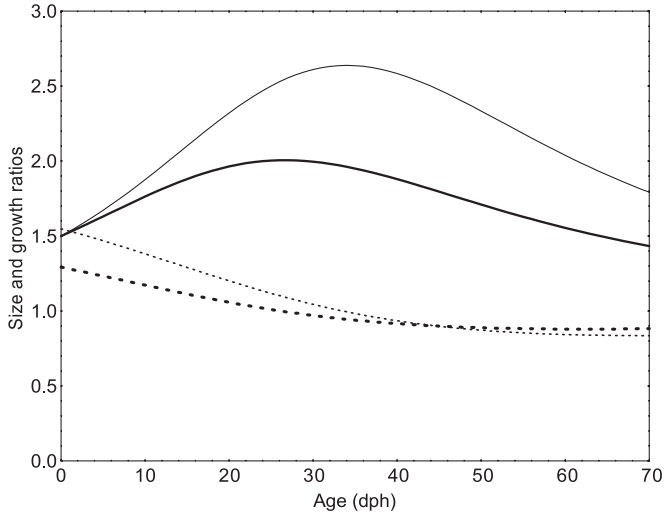
This study presents the first intraspecific evaluation of larval growth performance of a marine fish species across different experimental scales, environments, and regions. The development of STDG models based on larvae fed in excess has allowed the comparison of growth performances of larval groups from widely different systems and environments. Although temperature-dependent growth models for cod larvae have been presented earlier (e.g., Campana and Hurley 1989; Otterlei et al. 1999), they have been parameterized as age-based models and (or) have been based on data where feeding conditions have been confounded with temperature.

Fig. 5. Growth ratios from (*a*) laboratory, (*b*) enclosure, and (*c*) field studies (defined as the ratio of average observed daily growth rate versus average daily predicted growth rate). Numbers in the bars refer to the respective studies, with the lowest positioned number in a given bar referring to the study with the lowest value in that bar. The vertical line at 1.0 refers to the ratio where the observed average growth rate equals the predicted average growth rate.



Age-based models impose certain critical assumptions when the larvae have been growing at changing temperatures, since the age-at-size will need to be adjusted as the fish move from one temperature field to another. For example, a larva that has been growing at 8 °C will in the ATDG model need to be reassigned a younger age (at a given size) when it moves into warmer waters (or an older age if moves into colder waters) to obtain the correct size-at-age according to the ATDG model. The impact of changes in age-at-size within the original model specifications is unclear. Furthermore,

Fig. 6. Progression of size (solid lines) and growth ratios (dotted lines) (ratio of average observed value versus average predicted value) based on an above-average (upper; thick lines) initial weight (67.5 μg) or a below-average (lower; thin lines) initial weight (30 μg) relative to a mean initial weight (middle) of 45 μg. Simulations are run at 6 °C constant temperature. dph, days posthatch.



models based on field-sampled material where temperature and potentially confounding factors such as food level and larval size effects are not separated (Campana and Hurley 1989) are not well suited as reference growth curves either. One of the advantages of comparing the observed size-at-age with the temperature-dependent growth potential from STDG models is that the residuals can possibly serve as indirect measures of feeding conditions during the larval period.

Comparisons with several laboratory studies confirm that the underlying data for the models represent some of the most rapid laboratory growth rates for cod available after 25 years of cod larval culture. As such, the models should have utility for predicting the temperature- and size-dependent growth potential of cod larvae. The comparison of observed versus predicted growth in enclosure studies also supports the applicability of the STDG models. Enclosure systems typically have been characterized by high growth and survival rates in the absence of predators when food levels have been in excess of 10 prey·L^{-1} (Øiestad 1984, 1990). The close correspondence between enclosure observations and predictions further suggests that the STDG outputs are realistic estimates of larval growth potential in cod.

Growth performance of field-caught larvae

Consistent with expectations, the surviving cod larvae from the field seem to have been growing at rates close to their estimated capacity. This is the case for populations from both sides of the Atlantic and from several years of study (e.g., Suthers and Sundby 1993; Meekan and Fortier 1996). Incorporation of temperature in the growth models seems to explain to a large extent the difference in size-at-age reported by Suthers and Sundby (1996). Temperature-mediated differences in growth were also indicated between years (Meekan and Fortier 1996). In their study, the higher growth rate found for the 1992–1993 cohort also initially ex-

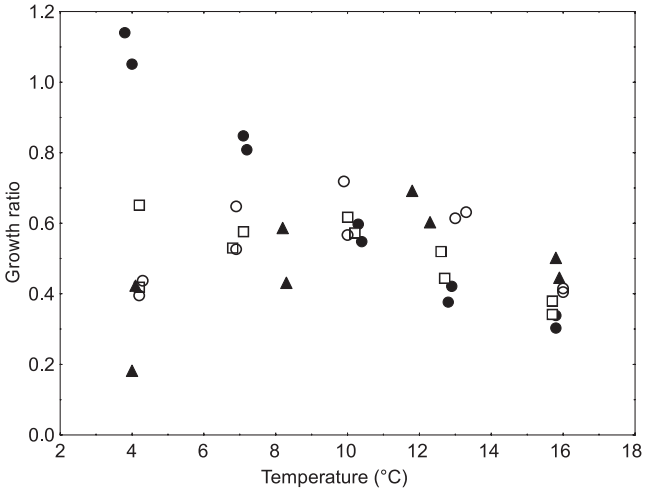
perienced higher temperatures than the 1991–1992 cohort. The finding that a stronger selection for survival took place in the warmer year is still worth noting, since the fish will be more susceptible to starvation-related mortality during food shortage at high-temperature conditions compared with at low-temperature conditions (McGurk 1984). The selective mortality took place after day 40 from hatching at a larval size greater than 10 mm (Meekan and Fortier 1996), however, and at this size, predation mortality may be more important than starvation as a mortality agent. Since no data on selective mortality were available from other field studies, it is not possible at this stage to conclude whether the high growth of the survivors is due to generally high growth rates or if this is the result of a very strong selection for larger size-at-age.

Internal and external influences on larval growth

Several studies have previously shown larval mortality to decrease with larval size (Bailey and Houde 1989; Houde 1997), and mortality rates in fish larvae have been suggested to be especially high considering their size (McGurk 1986). The finding that surviving cod larvae seem to be growing at rates close to their maximum capacity may reflect the importance of growing fast during the larval stage. This may not always be the case with smaller larvae, however. Buckley et al. (2004) sampled larvae smaller than 10 mm on the Georges Bank and concluded, using RNA/DNA ratios as indirect measures of recent growth, that larvae found at temperatures around 8 °C were growing slower than those at 7 °C. The question still remains if these larvae at higher temperatures suffered subsequent higher mortalities and failed to contribute to recruitment. Since fish larvae typically do not deposit significant amounts of energy storage in livers and muscle as do older fish, the resilience of larvae to starvation mortality does not improve much during the larval stage (Hunter and Coyne 1982; Jordaan and Brown 2003). Thus, a food shortage, especially at relatively high temperatures, can rapidly result in increased mortality. This does not have to imply direct starvation mortality, since elevated temperatures may increase the consumption of co-occurring predators as well.

The population genetic effects on the temperature relationship are still largely unresolved. Relatively small differences were observed between NA cod and NC cod, and contrary to the predictions from the countergradient hypothesis (Conover and Schultz 1997), offspring from the northern stock grew slower than the southern (NC cod) offspring (Otterlei et al. 1999). The difference in growth between offspring from the two stocks was comparable with the growth difference caused by a 0.5 °C difference in rearing temperature. The diversity of the genetic material underlying these studies is small, however, and broader parental coverage is needed before this matter can be properly resolved. As pointed out by Suthers and Sundby (1996), environmental factors other than temperature may also influence the growth of cod populations. Cod stocks from the eastern and western side of the Atlantic experience up to 48% difference in day length, and this may also explain part of the differences in observed growth rates. Although prolonged day lengths have been shown to generate increased growth rates of larval cod in the laboratory (Puvanendran and Brown 2002), these effects are generally of a smaller magnitude than those generated by differences in ambient temperature. A growth ratio of 1.15 was obtained for larval groups reared at 24:0 versus 16:8 day length (Puvanendran and Brown 2002), while the estimated growth ratio was 1.40 between cod from the eastern and western Atlantic temperature environments, which had a 3–3.5 °C temperature difference in addition to the same day length difference of approximately 50% (Suthers and Sundby 1996). The apparent applicability of the NC cod STDG model across regions and populations therefore suggests ambient temperature to be a major contributor to differences in growth rates between populations. Further investigations into differences in population-specific growth responses are strongly encouraged, however, since such differences have been documented in other species (Conover and Schultz 1997).

Fig. 7. Growth ratios at different temperatures from short-term experiments by Steinarsson and Björnsson (1999). Different symbols refer to larval groups with different initial weights: 0.046 mg (●), 0.107 mg (□), 0.140 mg (○), and 0.095 mg (▲).



Model evaluation and comparison

None of the originally selected cod growth papers enabled a comprehensive comparison of model performance across the entire reported temperature range. In a series of short-term experiments, however, Steinarsson and Björnsson (1999) reared young cod larvae at temperatures ranging from 3.8 to 16.0 °C. Although these experiments did not meet the selection criteria for individual growth studies used here (owing to short duration), the data from Steinarsson and Björnsson (1999) enabled a comparison with the STDG model across the entire temperature range. Comparing growth performances from their experiments with predicted growth performances from the STDG model reveals a wider range in performances at 4 °C and a relatively lower growth performance at 16 °C (Fig. 7). Overall, the growth rates in these experiments were substantially lower than predicted by the model, with growth ratios averaging about 0.6. This is most likely not due to the origin of larvae (from Icelandic populations), since larvae sampled from Icelandic waters were growing as fast as the model predictions (Begg and Marteinsdottir 2000). Two of the data series had the highest growth ratios at around 10 °C, while the two others had the highest growth ratios at 4 and 12 °C, respectively. The highest mortality

rates were also observed at 16 °C (Steinarsson and Björnsson 1999), suggesting that for young cod larvae, temperatures above 14 °C are suboptimal for growth and survival. Temperatures above 12 °C have previously been shown to be detrimental to developing cod embryos, while the tolerance to higher temperatures increases after hatching (Iversen and Danielssen 1984). At temperatures below 14 °C, the average growth ratios predicted from the STDG model were relatively constant and averaged 0.54–0.62 throughout the 4–14 °C temperature range (data grouped in 4, 7, 10, and 13 °C temperature groups; Kruskal–Wallis test, $p > 0.8$, Kruskal–Wallis test, $p < 0.05$ when including the 16 °C group). Although noticeable variability in growth ratios was observed between groups in these short-term experiments, the overall similar growth ratio in the temperature range 4–14 °C suggests that the temperature effect of the STDG models was appropriately parameterized.

The predictions from the Campana and Hurley (1989) model stand out as the case where cod larvae at sea are growing relatively slowly compared with their growth potential. This study was the first of its kind, linking the ambient temperature history of field-caught larvae with an age-based model. There are some potential methodological problems with the data material underlying the construction of this model. Samples were taken with 0.61-m Bongo nets, a gear not suitable for quantitative sampling of cod larvae larger than 10–12 mm (Campana and Hurley 1989; Suthers and Frank 1989). Larger larvae are underrepresented in the samples, and it is thus not surprising that growth rate apparently declines rapidly with age. To what extent this avoidance effect is confounded by temperature is unclear, but since the larger individuals will be very important in determining the apparent growth rate at older ages, further investigations into this matter are strongly recommended. The initial larval size used by Campana and Hurley (1989) is 3 mm TL, which was significantly smaller than sizes reported by Bolz and Lough (1988) for cod larvae in the same area. Although Campana and Hurley (1989) considered the Bolz and Lough (1988) correction of 30% shrinkage to be excessive, comparisons with length measurements of live cod larvae in the laboratory that typically are between 4 and 5 mm TL at hatch (e.g., Folkvord et al. 1999; Puvanendran and Brown 1999), seem to support the correction used by Bolz and Lough (1988). The implication of the Campana and Hurley (1989) model is that cod larvae are increasingly food limited with increasing temperature. This still may be a valid point (Buckley et al. 2004), but to what extent these larvae survive to older stages still remains an open question. The fact that the Campana and Hurley (1989) model does not permit cod to grow beyond 18 mm at 9 °C indicates limitations of the model. This is not an unrealistic ambient temperature for cod to experience during their early juvenile stage in the Georges Bank area. On the other hand, the STDG model supports the growth pattern presented in Bolz and Lough (1988) during the first 90 days after hatching, suggesting that the predictions based on the Campana and Hurley (1989) model underestimate growth, especially during the latter part of the study period.

The apparent high growth rate of field-caught cod at low temperatures also needs some clarification. Since the estimated ages used in these studies are based on otolith microstructure analysis, there is a possibility of age underestimation due to slow otolith growth (Otterlei et al. 2002). Studies of the otolith growth of the larvae used to parameterize the STDG and ATDG models have shown that the daily incremental growth at temperatures below 6 °C is very narrow and well below the practical resolution limit of light microscopy analysis (Otterlei et al. 2002). At 4 °C, the average daily radial otolith growth during the first 3 weeks was less than 0.4 μm. The groups from the colder regions and years in the papers by Begg and Marteinsdottir (2000) and Anderson and Dalley (2000) both originated in temperatures around or below this level. A significant underestimation of age is thus possible, where apparent growth will incorrectly be confounded by initial ambient temperature. In the case of the study of Begg and Marteinsdottir (2000), a positive growth effect of the northern stocks may partly be due to longer periods of daylight for feeding (Suthers and Sundby 1996). The possibility that population-specific growth performances exist cannot be ruled out either (see above), but the laboratory experiments with offspring from the same stocks (Laurence 1978; Steinarsson and Björnsson 1999; Puvanendran and Brown 2002) do not provide evidence of offspring from these stocks responding differently to temperature or performing better than predicted by the STDG model.

Although the STDG model in general predicted the growth pattern with good accuracy, there are a few data series that warrant further comments. The observed size-at-age in Finn et al. (2002) was lower than expected initially and vice versa at the end. For the latter, it should be noted that the data at this point are outside the main model domain. As such, the growth capacity of larger individuals may well be higher than predicted by the model. An indication of this being the case is also present in a data set with even higher rearing temperatures (1992 data from van der Meeren et al. (1994), which were outside the size and temperature range of model). Shifts in temperature for maximum growth have also been shown in cod and other species (Hallaråker et al. 1995; Otterlei 2000), and the early juvenile cod may thus have a higher growth potential than predicted by the model at temperatures above 10 °C. However, a similar pattern as observed in Finn et al. (2002) may also to some extent be created by sampling effects. Selective sampling of smaller individuals is a common problem in cylindrical bag enclosures owing to the lack of suitable sampling gear, and in many cases, the final sizes at termination of the experiment are the only unbiased estimates of size-at-age (T. van der Meeren, Institute of Marine Research, Austevoll, 5392 Storebø, Norway, personal communication). In a recent paper by van der Meeren and Moksness (2003), larger than expected larvae were found initially in similar-type enclosures. Consequently, this discrepancy does not seem to be related to rearing in bag enclosures as such. In addition, group-specific growth responses may very well vary from the average deterministic predictions from the STDG model. Periods of relatively low growth may be compensated for by extraordinary high growth rates, as have been documented for adult cod (Pedersen and Jobling 1989). At the same time, fast growth events caused by development or improvements in food availability may continue for several subsequent days, resulting in a noticeable growth burst (Juanes and Conover

1994). These effects are expected to be more pronounced at smaller time scales, however, and integration of growth over longer time periods is expected to more accurately reflect the overall true growth performance.

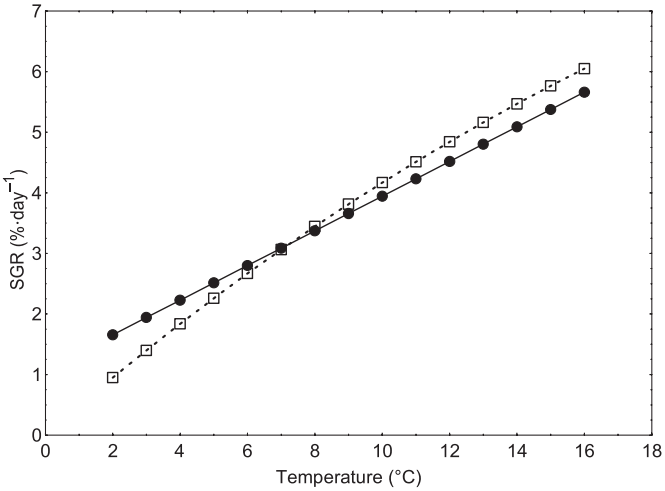
A special consideration is given to the initial sizes of larvae used in the field studies, since these are usually unknown. In this paper, an initial weight of 45 μg was used (yolk excluded), and this represents a relatively heavy embryo at hatching. Using a lower initial weight in field examples would increase the estimates of cod larvae growth in the field. With respect to the main conclusions of this paper, this strengthens the claim that the surviving larvae are indeed growing very well. When plotting the effects of a 50% increase of initial weight, we can see that the relative size difference increases initially. This is due to the increasing growth rate with size up to the size at maximum growth rate (about 0.7 mg DW for both NA and NC cod). As the larvae pass the size of maximum growth capacity, the relatively smaller larvae tend to catch up somewhat as the growth of the larger larvae slows down. A size-specific growth rate pattern like this would also generate an increase in the coefficient of variation with size in a cohort of larvae followed by a decrease in the coefficient of variation for the same reasons (Huston and DeAngelis 1987). Thus, one should be careful about inferring selective mortality based only on patterns in mean–variance relationships (Miller 1997). It can be noted that the size ratio will converge as the age of comparison increases, however, and by day 60, the relative size difference between the mean initial weight and a lower initial weight is back to what it was at the outset. The differences in growth rates have also stabilized, and the growth ratio calculations are therefore quite robust against variations in initial size.

An indication of the robustness of the STDG models to predictions at the outer range of the model domain can be found by comparing them with other model predictions. Björnsson and Steinarsson (2002) presented a model for juvenile and adult Icelandic cod based on experiments where the fish had been fed in excess. Their model was applicable for juveniles with a wet weight of 1–2 g up to adult cod weighing several kilograms. The STDG models and the Björnsson and Steinarsson (2002) model yielded comparable growth estimates at a fish size of 450–600 mg DW, which were the sizes of minimal growth predicted by the STDG models (Fig. 8). The differences in estimated daily specific growth rates were less than 0.4% for the NA cod model and less than 1% for the NC model at temperatures of 4–16 °C. This may facilitate the generation of growth trajectories from hatching to spawning by using the STDG models until 450–600 mg DW and the Björnsson and Steinarsson (2002) model thereafter.

Final remarks

This study has shown that ambient temperature is an important factor in determining the size-at-age of larval cod in natural cod stocks. Previous studies have shown that juvenile cod size at the 0-group stage are strongly correlated with regional temperature indices (Ottersen and Loeng 2000). I suggest that these correlations may be determined during the larval stage owing to the marked temperature-dependent growth at this stage. The growth response to temperature in

Fig. 8. Comparison of temperature-specific growth predictions for northeast Arctic Atlantic cod (*Gadus morhua*) of 450 mg using the size- and temperature-dependent growth model (●) and the model presented by Björnsson and Steinarsson (2000) (□). SGR, specific growth rate.



fishes is most pronounced at early stages (Post and Lee 1996), and thus, changes in ambient temperature during these stages may generate large growth differences that carry on into later stages. Temperature versus recruitment correlations have been found to vary with region in cod, where positive correlations are found in northern, colder waters, while the correlation tends to be negative at the southern borders of the cod distributional area (Planque and Frédou 1999). A lower recruitment of cod in the North Sea is seen in relatively warm years (Beaugrand et al. 2003), and the plankton concentration is shown to be inversely related to ambient temperature. It is suggested that this will reduce larval and early juvenile survival owing to increasing metabolic costs at times when plankton energy is in short supply. Whether this reduced survival is accompanied by a reduced growth of the survivors (recruits) remains to be documented. On the other hand, the NA cod stock will typically benefit from higher temperatures caused by increased advection of relatively warm Atlantic water with abundant suitable plankton (Sundby 2000). Significant growth responses to climatic changes thus seem likely as surviving cod respond to improved feeding conditions and elevated temperature conditions.

In summary, the development of the STDG models enabled a broad comparison of growth performance of the youngest stages of cod. The results so far indicate that the surviving larvae have been growing at rates close to their maximum temperature- and size-dependent capacity, but several questions still remain. How common is a temperature-dependent mortality risk due to increased energetic demands in cod larvae? To what extent are there population differences in responses to temperature? What are the consequences of climate changes on growth and recruitment variability in this species? For all of these questions and many more, the documentation of the growth potential and to what extent this is achieved under the prevailing conditions should enable us to provide more qualified answers as well as new challenging questions.

Acknowledgements

I am indebted to Dr. Erling Otterlei and Gunnar Nyhammer, who took on the effort of extensive cod rearings in the laboratory. Prof. Gudrun Marteinsdottir and Dr. Geir Blom, Dr. Larry Buckley, Dr. Nigel Finn, Dr. Torstein Pedersen, Dr. V. Puvanendran, Dr. Iain Suthers, and Dr. Terje van der Meeren are thanked for providing additional information from their publications and Prof. Ken Frank for providing references to Canadian hydrography data. This study was supported by Norwegian Research Council grants 108920/120 and 130192/140 and a study leave grant from the University of Bergen to the Chesapeake Biological Laboratory, University of Maryland. The paper benefited from discussions with members of the ICES WG in recruitment processes and by constructive comments by Prof. Ed Houde, Dr. Tom Miller, and Clelia Booman.

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