Temperature- and size-dependent growth of larval and early juvenile Atlantic cod (*Gadus morhua*): a comparative study of Norwegian coastal cod and northeast Arctic cod

Erling Otterlei, Gunnar Nyhammer, Arild Folkvord, and Sigurd O. Stefansson

Abstract: Norwegian coastal (NC) and northeast Arctic (NA) Atlantic cod (*Gadus morhua*) larvae were reared on live zooplankton to investigate temperature- and size-specific growth. Larval and juvenile growth was temperature and size dependent. Growth in length and weight increased with increasing temperature from 4 to 14°C, with a corresponding reduced larval stage duration. Maximum growth rate occurred at a larval size of 0.1–1.0 mg dry weight, followed by a declining trend during the juvenile stage. The temperature optimum of larval cod fed in excess is estimated to be between 14 and 16°C, with a maximum weight-specific growth potential exceeding 25%·day^{-1}. Temperature- and stock-specific growth curves of dry weight at age are well described by a generalized Gompertz model. A stock-specific difference in mean weight at age was observed, with NC growing better than NA. Neither countergradient latitudinal variation in growth capacity of the two larval cod stocks nor temperature adaptation across latitudes was indicated. A stock-specific difference in weight at length was observed in early juveniles, with NC being heavier than NA. Overall, a positive correlation between temperature and condition level was found. No distinct temperature- or stock-specific differences in survival were observed.

Résumé : Des larves de morue (*Gadus morhua*) provenant des côtes de Norvège (CN) et du nord-est de l'Arctique (NA) ont été nourries de zooplancton vivant dans le but d'étudier leur croissance en fonction de la température et de la taille. La croissance des larves et des juvéniles était fonction de la température et de la taille. La croissance en longueur et en poids augmentait en fonction de la température dans la gamme de 4 à 14°C et il en résultait un raccourcissement correspondant de l'étape larvaire. Le taux de croissance maximum a été noté au poids larvaire de 0,1–1,0 mg (poids sec), qui était suivi d'une tendance à la baisse pendant l'étape juvénile. La température optimale où les larves se nourrissaient en excès a été estimée comme entre 14 et 16°C, le potentiel de croissance pondéral maximum spécifique excédant 25%·jour^{-1}. Les courbes de croissance spécifiques à la température et au stock par poids sec et âge sont bien décrites par un modèle généralisé de Gompertz. Un écart spécifique au stock du poids moyen selon l'âge a été observé, la croissance des larves CN étant supérieure à celle des NA. Il n'a pas été noté de variations contre-gradient en latitude de la capacité de croissance des larves des deux stocks ni d'adaptation à la température en fonction de la latitude. Un écart du poids selon la longueur spécifique au stock a été noté au début du stade de juvénile, les CN étant plus lourds que les NA. De façon générale, il existait une corrélation positive entre la température et la condition. Aucun écart distinct spécifique à la température ou au stock n'a été observé pour la survie.

[Traduit par la Rédaction]

Introduction

Recruitment in most marine fishes is characterized by high fecundity (Mertz and Myers 1996) and subsequent high mortality during early life stages (Bailey and Houde 1989; Houde and Zastrow 1993). Variability in growth and mortality is known to cause fluctuations in recruitment (Houde 1989, 1997*a*, 1997*b*; Pepin and Myers 1991). The growth and mortality of marine fish larvae depend on temperature, body size, and food availability (Houde and Zastrow 1993). From an evolutionary point of view, it is widely argued that growth should be maximized during the early life of fishes; the so-called "growth–mortality" hypothesis (Hare and Cowen 1997). This hypothesis postulates that larger (e.g., Bailey and Houde 1989), faster growing, and more rapidly developing individuals have a higher probability of survival (Hare and Cowen 1997). Thus, rapid growth may reduce the risk of mortality in larval stages (e.g., Miller et al. 1988) by reaching a larger size at any given age.

Temperature influences metabolic processes and, besides prey availability, is the single most important factor that determines growth rates in fish (Brett 1979). Although the influence of temperature on the growth of Atlantic cod (*Gadus morhua*) has been studied for many years (Jobling 1988), knowledge of the temperature- and size-dependent growth of

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larval and early juvenile stages is limited (e.g., Leising and Franks 1999). Laurence (1978) found growth of larval cod to be positively correlated with temperature in the range 4–10°C. Upper lethal temperatures through the yolk-sac stage ranged from 15.5 to 18°C for larvae acclimated to 7–9°C (Yin and Blaxter 1987). A few temperature-dependent models have been developed, simulating the larval and early juvenile growth for cod on Georges Bank (Campana and Hurley 1989; Leising and Franks 1999). However, there are few laboratory studies on the temperature-dependent growth of larval cod (exception Laurence 1978), and the estimation of the temperature effect is thus uncertain (Leising and Franks 1999). Recent mesocosm studies of larval cod (e.g., Blom et al. 1991, 1994*a*; Folkvord et al. 1994) were all influenced by covarying temperature and food conditions.

Few metabolic relationships are independent of size (Brett 1979). Growth is no exception and it decreases with increasing body size (Jobling 1988; Brander 1995). Although considerable variation in weight-specific growth rate (G) has been reported, with G ranging from <1 to 79%·day^{-1} (Houde and Zastrow 1993), fish larvae are characterized by high potential G relative to larger fish. Growth rates exceeding 20%·day^{-1} have previously been reported for larval cod (e.g., van der Meeren et al. 1994). Temperature optima (T_{opt}) for maximum growth (G_{max}) of fish may show an ontogenetic shift, with larvae and juveniles often having a higher T_{opt} for growth than larger conspecifics (McCauley and Huggins 1979; Jobling 1994). However, it has been suggested that yolk-sac larvae of cod have lower T_{opt} than juveniles and adults (Jobling 1988).

Throughout the area of distribution in the North Atlantic, the numerous cod stocks inhabit regions subject to a wide range of environmental conditions (Brander 1995). Differences among Norwegian coastal (NC) and northeast Arctic (NA) Atlantic cod in growth performance (van der Meeren et al. 1994; Svåsand et al. 1996), genetic (e.g., Møller 1968), meristic, and otolith characteristics (e.g., Rollefsen 1934) have been demonstrated. However, considering the economic and ecological importance of cod, links between genetic characteristics of a specific cod population and growth performance under varying environmental conditions are generally unknown (Svåsand et al. 1996).

The purpose of this study was to characterize temperature- and size-dependent growth of cod larvae and juveniles. An age- and temperature-mediated growth model has been developed, based on the Gompertz equation (Zweifel and Lasker 1976). NC and NA were reared together under identical conditions at temperatures from 4 to 14°C, and the growth and survival patterns of the two stocks were compared. The study was motivated by the hypothesis that the growth patterns of the stocks reflect temperature adaptation across latitudes and that a countergradient latitudinal variation in the growth capacity of the larval cod stocks (i.e., that the genetic capacity for growth varies inversely with the length of the growing season across a latitudinal gradient; Conover et al. 1997) is expected.

Materials and methods

Biological material

NC and NA eggs were naturally spawned in pens (120 m^3) and tanks (5 m^3) in early spring during two seasons (5 April 1995 and 14 March 1996) at the Parisvatnet, Øygarden, and Austevoll aquaculture research stations in western Norway. The broodstocks, 40–100 fish in each population, had been kept in captivity for about 3 years, with the exception of the wild-caught NC spawners utilized in 1996. The NA broodstock originated from wild fish captured in the Lofoten area in northern Norway (68°N) during the 1992 spawning season (Svåsand et al. 1996), and the NC stock originated from western Norway (60°N). The fertilized eggs, a sample of 0.3 L of each stock, were incubated separately in 70-L aerated black conical tanks at 7.3–7.9°C and 32.9–33.8‰ salinity at the Bergen High Technology Center. In both seasons, 50% hatching occurred 12 days after fertilization, referred to as day 0 of larval age.

Experimental design

Two experiments with similar design were undertaken in 1995 and 1996. Initial stocking densities were 1400 larvae, 700 NC and 700 NA, per tank. The 2-day-old yolk-sac larvae were individually counted and randomly distributed into replicate green square fiberglass tanks of 500 L. In 1995, the fish were reared for 8 weeks at three different temperatures (±SD), 4.1 ± 0.2, 8.0 ± 0.1, and 12.0 ± 0.2°C, and in 1996 at 6.1 ± 0.1, 10.0 ± 0.2, 12.0 ± 0.3, and 14.1 ± 0.2°C. Another 100 larvae of each stock were kept in separate 5-L pails as viability groups at the respective temperatures. All larvae were acclimated to the rearing temperatures for 1 day, except for the fish at 12 and 14°C in the 1996 experiment, where the temperature was gradually increased over a period of 5 days. In order to distinguish NC from NA in 1995, we marked the otoliths of the latter stock with alizarin complexone (100 mg·L^{-1} for 24 h) 2 days before hatching, whereas in 1996 the NC larvae were marked (Blom et al. 1994*b*).

Feeding conditions

Larvae and juveniles were fed live natural zooplankton one to five times a day. Larvae <12 mm standard length (SL) were offered a fraction of zooplankton ranging from 80 to 250 µm, juveniles in the range of 12–15 mm were given plankton 80–350 µm, and fish >15 mm were fed zooplankton varying in size from 80 to 2000 µm (mainly copepods). Zooplankton density was sampled daily in each tank (before feeding), and the plankton were counted and categorized into six main groups: small tintinnids, rotifers, and nauplii and the larger calanoid, cyclopoid, and harpacticoid copepodites and copepods. Beginning on day 3, all tanks received an equal amount of zooplankton, more of which was later added to maintain a similar prey density above 1000 individuals·L^{-1} in each rearing unit. Cultivated algae (2–4 L of each species), *Isochrysis galbana* and *Rhodomonas baltica*, were added to each tank three to seven times a week. Tintinnids and rotifers dominated the supplied plankton early in the 1995 experiment, whereas copepod nauplii later became most abundant. The zooplankton diversity in 1996 was initially dominated by copepod nauplii and thereafter by copepodites as fish larvae started to metamorphose. The prey density in tanks decreased as the juveniles grew beyond 15 mm and preyed mainly upon larger copepods.

Rearing conditions

A simulated natural light regime for the latitude of Bergen (60°25′ N) was utilized. Maximum photoirradiance in the surface of the water was 1.8–3.5 µE·m^{-2}·s^{-1}. Temperature was measured twice a day throughout the experiments. The water was gently aerated to reduce the patchiness of the prey and larvae. Oxygen concentration (percentage and milligrams per litre) was recorded daily and remained above 70% saturation, while salinity ranged from 30.9 to 33.5‰. Gas saturation, monitored on day 15 in 1995, indicated nitrogen supersaturation (105–107%) in the rearing tanks at

Table 1. Mean egg and larval sizes of NC and NA in 1995 and 1996.

	Stock			
Year	NC	NA	*n*	*p*
1995				
ED (mm)	1.27 (0.06)	1.31 (0.06)	100	<0.001
SL (mm)	4.23 (0.17)	4.24 (0.15)	70	ns
MH (mm)	0.24 (0.01)	0.25 (0.01)	70	<0.001
DW (mg)	0.027 (0.005)	0.029 (0.008)	20	ns
1996				
ED (mm)	1.40 (0.07)	1.37 (0.06)	100	<0.001
SL (mm)	4.68 (0.16)	4.82 (0.28)	70	<0.001
MH (mm)	0.28 (0.01)	0.27 (0.02)	70	ns
DW (mg)	0.034 (0.006)	0.033 (0.005)	20	ns

Note: *p* values refer to *t* tests comparing stocks. Egg diameter (ED) was measured on day 1 postfertilization. Standard length (SL), myotome height (MH), and dry weight (DW) of yolk-sac larvae were measured on day 2 posthatch. Values in parentheses represent the SD of the estimated parameters, and ns indicates $p > 0.05$.

12°C. The bottom of each tank was siphoned daily from day 14, and dead larvae and juveniles were removed and counted. Water exchange was about 2%·day^{-1} during the first 14 days after larval stocking and was increased to 5–30%·day^{-1} (depending on the biomass) throughout the experiments.

Sampling procedure

Initial samples of 70 yolk-sac larvae were taken on day 2 from each stock tank for estimation of live SL and myotome height (MH) under a dissecting microscope (Wild Heerbrug). Dry weight (DW) was recorded for 20 of these larvae. Another 30 larvae were routinely sampled in each tank once a week at daylight for similar measurements. The fish were transferred individually into marked vials, killed in liquid nitrogen, and stored at –80°C for subsequent otolith and DW analysis. The lapilli were removed and mounted on glass slides using clear varnish. Both lapilli were checked for alizarin marks and classified as either NC or NA using a fluorescence microscope (Zeiss Axioscope) at 200× magnification. The larvae or juveniles (n = 2172) were subsequently dried (60°C for 24 h or until stable) and weighed on a Sartorius microbalance (±1 μg). Lapilli were selected for a number of reasons (Meekan and Fortier 1996), and it was possible to detect the alizarin mark without further polishing.

With a few exceptions the larvae and juveniles sampled were analyzed for otoliths and their DW recorded. At 6, 10, and 14°C, only 20 of the 30 sampled larvae and juveniles from each replicate were analyzed and the remaining larvae were retained for other purposes. Another 3.8% (n = 95) of the sampled larvae and juveniles were excluded due to missing data on either otoliths or DW. Three tanks were terminated before the 1995 experiment ended due to high mortality, probably caused by nitrogen supersaturation (both replicates at 12°C on day 21 and one replicate at 8°C on day 28). Data from the 12°C group for that year were excluded from further analysis, since data from this temperature regime were available from the 1996 experiment. In 1996, one tank at 14°C was terminated on day 35.

Data analysis

The relationship between larval stage duration (D, days) and temperature (T, degrees Celsius) was described by a power function as

$$D = aT^{-b} \quad (1)$$

where a and b are estimated constants (e.g., Houde and Zastrow 1993). Larval stage specific survival was estimated according to Beyer (1989) and Houde (1997*a*):

$$N_1 = N_0\left(\frac{DW_1}{DW_0}\right)^{-\frac{M}{G}} \quad (2)$$

where N_1 and N_0 are the numbers of larvae alive at the end and beginning of the larval stage, respectively, bounded by dry weights $DW_1 \approx 1.3$ mg, mean DW at onset of metamorphosis, and DW_0, the initial larval weight (day 2). Parameter M is the daily instantaneous mortality rate and G is the daily weight-specific growth rate. The fish alive at the termination of the experiments were counted and sorted with respect to stock. Estimated total survival for the respective treatments was corrected for sampling mortality (i.e., estimated as the mean of the number of fish alive at termination of the experiment and the number of individuals alive at termination plus the number of larvae and juveniles sampled). Survival during the larval stage was estimated similarly, corrected for natural mortality recorded during the juvenile stage. Daily weight-specific growth rate G was calculated according to Houde and Schekter (1981):

$$G = 100(e^g - 1) \quad (3)$$

where the instantaneous growth coefficient g is

$$g = \frac{(\ln DW_2 - \ln DW_1)}{(t_2 - t_1)} \quad (4)$$

and DW is average dry weight (milligrams) on days t_1 and t_2, respectively. The shift in mean specific growth rate G with temperature T is described by the following regression:

$$G = a + bT + cT^3 \quad (5)$$

where a, b, and c are estimated constants (Jobling 1988). The length–weight relationships of ln-transformed data were described by the general allometric function

$$\ln DW = \ln a + b\ln SL \quad (6)$$

where a and b are constants (e.g., Pepin 1995). A second-order polynomial was fit to the residuals to test for departure from log-linearity (Pepin 1995). Only one third of the length–weight relationships analyzed were slightly nonlinear. Temperature- and stock-specific growth curves of DW with age were described by the Gompertz equation:

$$\ln DW(t) = C + Ae^{K(1-e^{-\alpha t})} \quad (7)$$

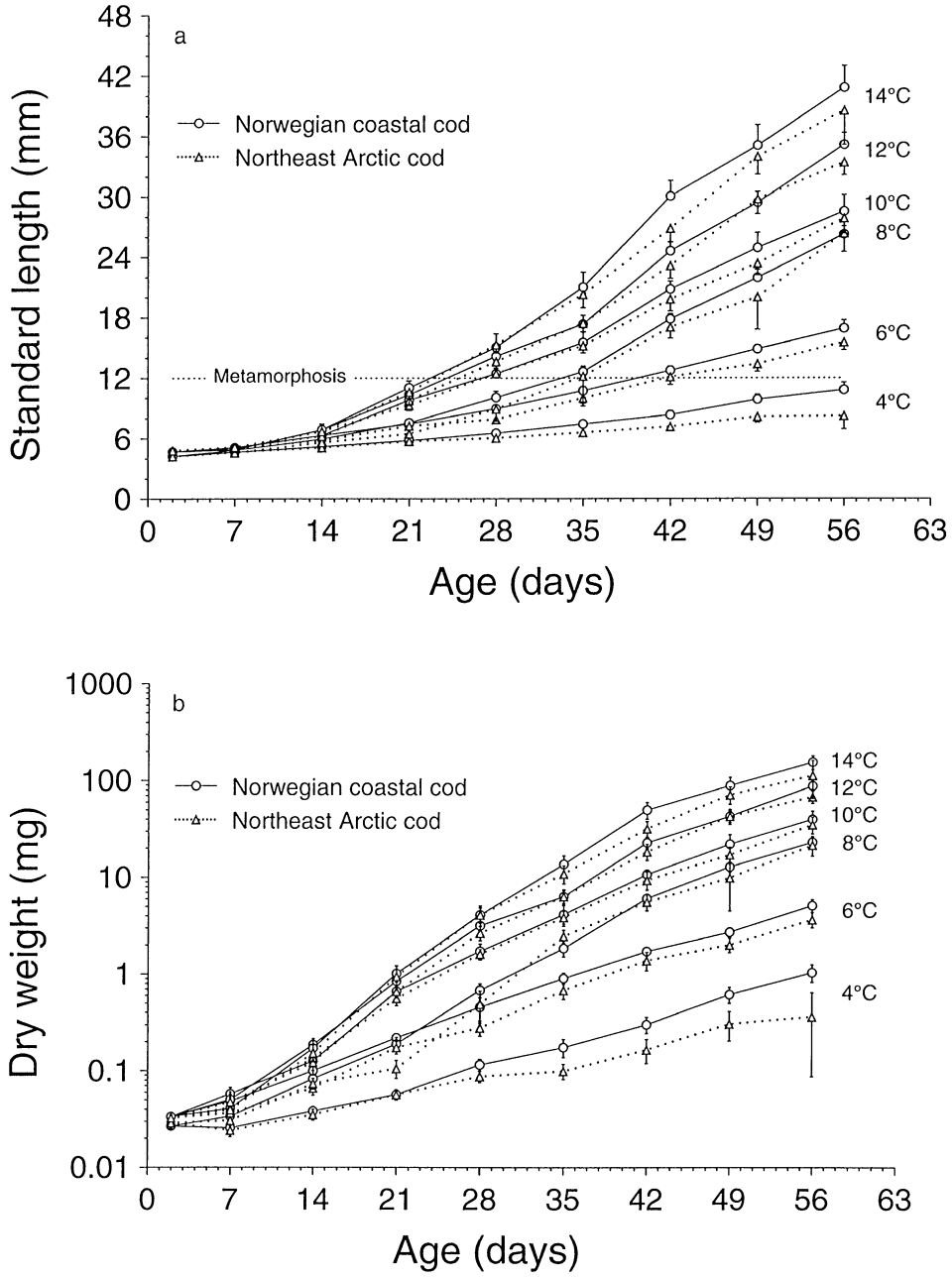
with DW (milligrams) at age t (days) and where C and A are constants, K is an expression of growth rate, and α is the rate of exponential decay (Zweifel and Lasker 1976). Parameters of the equation were estimated by nonlinear estimation. A generalized temperature-dependent growth model was created by substituting α with a linear temperature function and pooling data from the six different temperature regimes:

$$\alpha = a + bT \quad (8)$$

where a and b are constants and T is temperature. The procedure for further modifications (initiation, substitution, and reparameterization) of the Gompertz growth model is outlined in the Appendix. Finally, the current model was tested with independent growth data of larval cod from two mesocosm studies (Folkvord et al. 1994; Blom 1995).

Initial stock differences in egg diameter (ED) and larval DW, SL, and MH within a season were tested using Student's t test (Zar 1984), whereas a two-way ANOVA was employed for a similar ini-

Fig. 1. Mean size at age, (*a*) SL and (*b*) DW, of NC and NA reared at different temperatures. Vertical lines indicate 2 SE of the mean.



tial comparison between stock and seasons. For further growth comparison, data of replicates and seasons were combined (DW differed in 11% of the replicate *t* tests carried out). A two-way ANOVA was employed to estimate the effects of temperature and stock on mean DW and SL during the experimental periods. The data were checked for normality and the variance tested for heterogeneity using Hartley's F_{max} test. Data on DW and SL were ln transformed (Zar 1984). Significant ANOVAs were followed by a Tukey's (HSD) multiple comparison test to determine differences among treatments. In cases of significant interactions between factors, the treatments were split up and one-way ANOVAs were employed.

The effects of temperature on mean stock-specific growth rates were described by multiple regressions. Multiple comparisons of the length–weight regressions between treatments were tested with ANCOVA (Zar 1984). The ANCOVA was employed for overlapping size ranges: larvae (SL ≤ 10 mm, temperatures 4, 6, 10, 12, and 14°C) and juveniles (SL ≥ 14 mm, temperatures 10, 12, and 14°C). Larvae reared at 8°C differed significantly in slope from the other groups and separate stock-specific regressions were computed for this treatment. Effects were considered significant at a probability level of $\alpha < 0.05$.

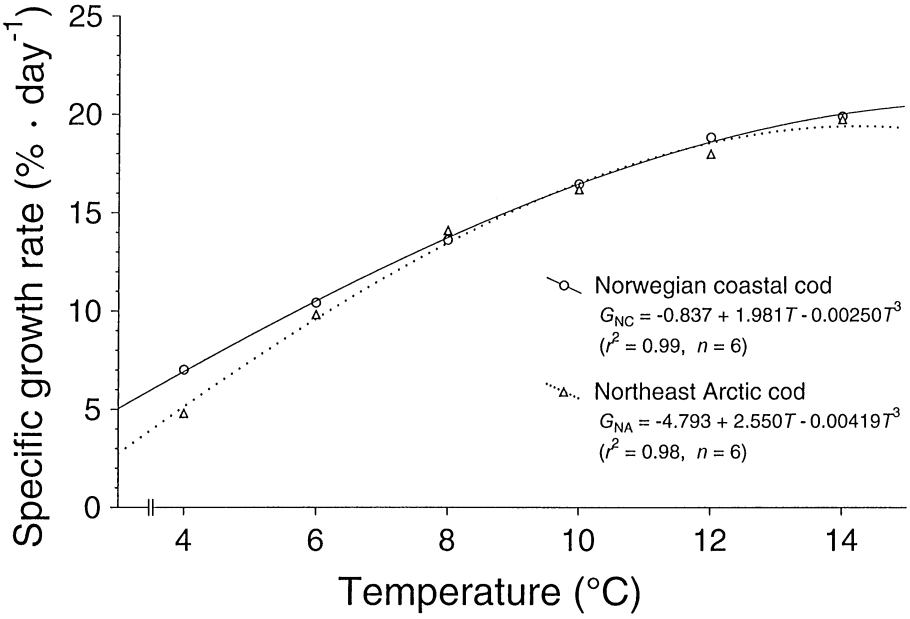
Results

Growth

Effects of temperature, stock, and fish size

Initial larval DW (day 2) of the two stocks was not significantly different (two-way ANOVA, $p = 0.76$). However, ED of both stocks was significantly smaller (one-way ANOVA, $p < 0.001$) in the late-spawned batches in 1995 compared with the earlier spawned egg batches used in 1996. Conse-

Fig. 2. Effects of temperature on mean weight-specific growth rates of NC and NA during the larval stage (SL ≤ 12 mm). Each point represents the mean growth rate of fish at the respective temperature.



quently, the initial larval DW was higher in 1996 (two-way ANOVA, $p < 0.001$) (Table 1).

Somatic growth in length and weight increased successively with increasing temperature from 4 to 14°C (Fig. 1). The final mean DW of all groups differed significantly (two-way ANOVA, $p < 0.001$) with the exception of the juveniles reared at 12 and 14°C ($p = 0.06$). Larval stage duration declined rapidly as temperature increased. Larvae reared at 14°C reached the onset of metamorphosis (12 mm SL) after 23 days compared with more than 56 days for fish at 4°C. The relationship between larval stage duration D and temperature was described by the following function: $D = 132.0T^{-0.685}$ ($r^2 = 0.97$, $n = 9$) for NC and $D = 152.9T^{-0.741}$ ($r^2 = 0.98$, $n = 9$) for NA. An increase in temperature from 6 to 12°C generated a 17-fold higher DW after 8 weeks. A stock-specific difference in mean DW at age was observed, with NC generally growing significantly faster than coreared NA from day 7 onwards (two-way ANOVA, $p < 0.001$). Mean DW and SL of NA were at most 27.0 and 7.4% lower, respectively, than those of NC at the end of the experiments at any given temperature.

Larval and juvenile weight-specific growth rates G were temperature and size dependent. Mean G increased with increasing temperature from 4 to 14°C. The T_{opt} for G_{max} of larval cod fed in excess was estimated at 16.2 and 14.2°C for NC and NA, respectively (Fig. 2). The G also increased transiently with increasing larval weight at all temperatures (Fig. 3). The G reached a peak at a larval size of 0.1–1.0 mg DW and then declined during the juvenile stage. Estimated G_{max} in both NC and NA larvae exceeded 25%·day^{-1}. Temperature had relatively little effect on larval mean G between 10 and 14°C ($Q_{10} = 1.6$, equal for both stocks). The effect of temperature was greater ($Q_{10} = 3.1$ and 3.5 for NC and NA, respectively) at lower temperatures from 6 to 10°C during the larval stage.

Function of age

Larval DW was modeled as a function of age and temperature, expressed as a modification of the Gompertz equation (Appendix, eq. A4):

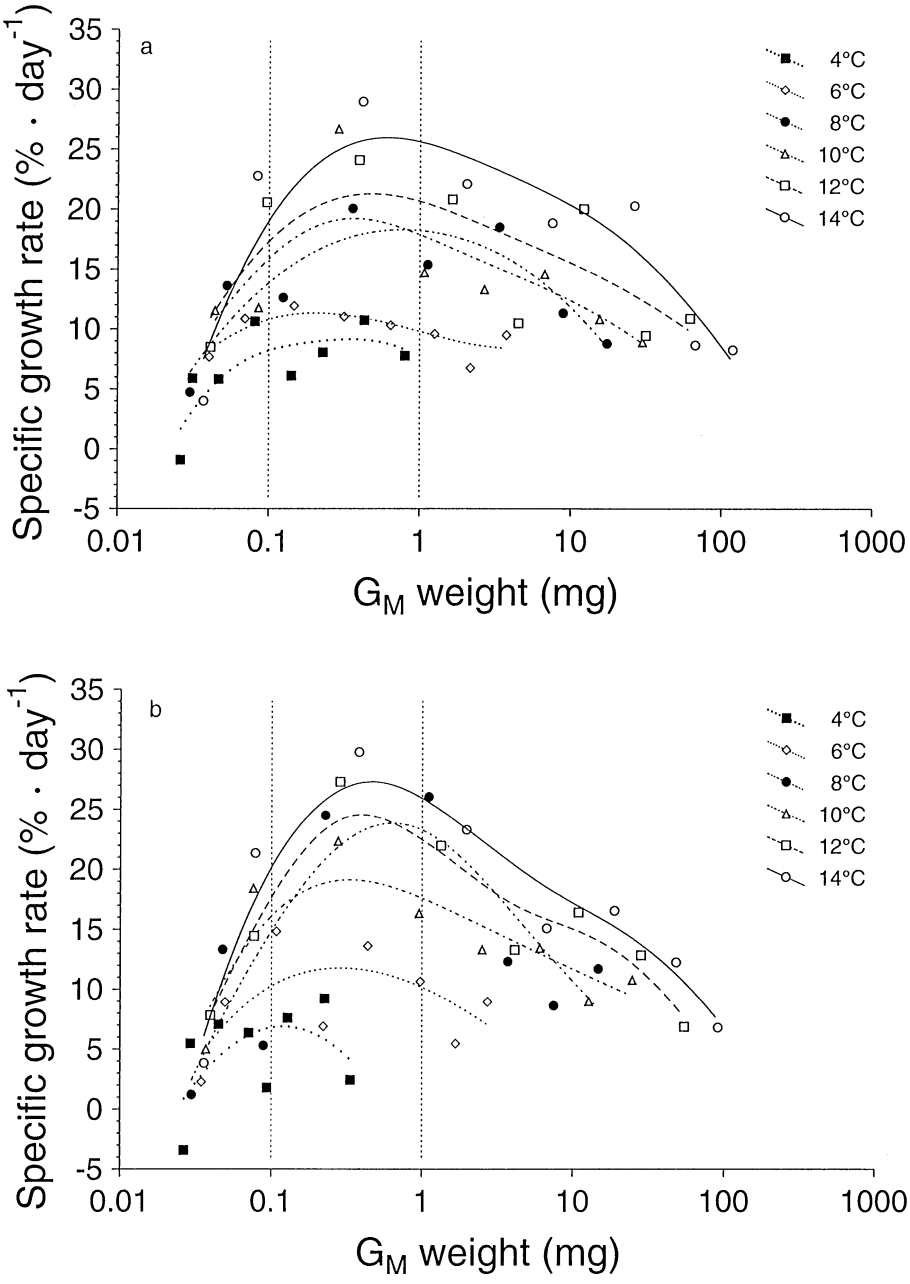
$$\ln \mathrm{DW}(t) = \ln \mathrm{DW}_0 - A + A \times \left(\frac{\ln \mathrm{DW}_\infty - \ln \mathrm{DW}_0 + A}{A} \right)^{(1-e^{-(a+bT)t})}$$

The fit of the data was good for both stocks ($r^2 = 0.95$ and $r^2 = 0.94$ for NC and NA, respectively) (Table 2). Although the initial DW was similar between stocks, predicted DW at age was consistently higher for NC than for NA (Fig. 4). Predicted mean DW of larvae on day 7 ranged from 35 to 65 μg and largely overlapped the range of the observed data, 24–56 μg (Table 3). As the experiments proceeded, the estimated values tended to be higher for the larvae reared at 4°C compared with the observed data, whereas the opposite occurred at 6°C and during the latter part of the experiment at 8°C. An estimated G_{max} of 26%·day^{-1} on days 18–20 for both stocks reared at 14°C agrees with the observed data (Figs. 3 and 5). Furthermore, the predicted peak in G of 8–9%·day^{-1} on days 51–56 for the stocks at 4°C is in accordance with our observations. The current model for the NC stock slightly underestimated the growth for larvae <1.5 mg DW, tested with independent data sets of larval cod from both of the two mesocosm studies (Fig. 6). The difference between the observed and estimated larval weight constituted <1–4 days of growth at the respective temperature.

Length–weight relationships

The length–weight relationships of cod indicate positive allometric growth at both the larval and juvenile stages ($b > 3$). An ontogenetic shift in the length–weight ratio occurred at the onset of metamorphosis (Fig. 7). Even though the early juveniles continued to increase in weight at a greater rate than in length ($b = 3.66$), the relative ratio decreased compared with the larval stage ($b = 4.01$ and $b = 4.14$ for NC and NA, respectively). A stock-specific difference in

Fig. 3. Weight-specific growth rate versus geometric mean DW of (*a*) NC and (*b*) NA larvae and juveniles reared under different temperature regimes. The fitted lines (least squares) indicate the general trends in growth. Data from replicates are combined.



weight at length was observed in early juveniles, with NC being heavier than the NA stock (ANCOVA, $p < 0.001$). Larval cod significantly differed in stock-specific slopes with regard to weight at length ($p < 0.05$) and were not comparatively tested. However, within both stocks the weight at length of larvae and juveniles significantly increased with temperature (ANCOVA, $p < 0.001$), indicating a positive correlation between temperature and condition level (Table 4). Larvae reared at 12°C were 49% heavier than larvae of similar length at 4°C. Only larvae reared at 14°C differed from this trend, showing an intermediate condition level.

Mortality and the *M*/*G* ratio

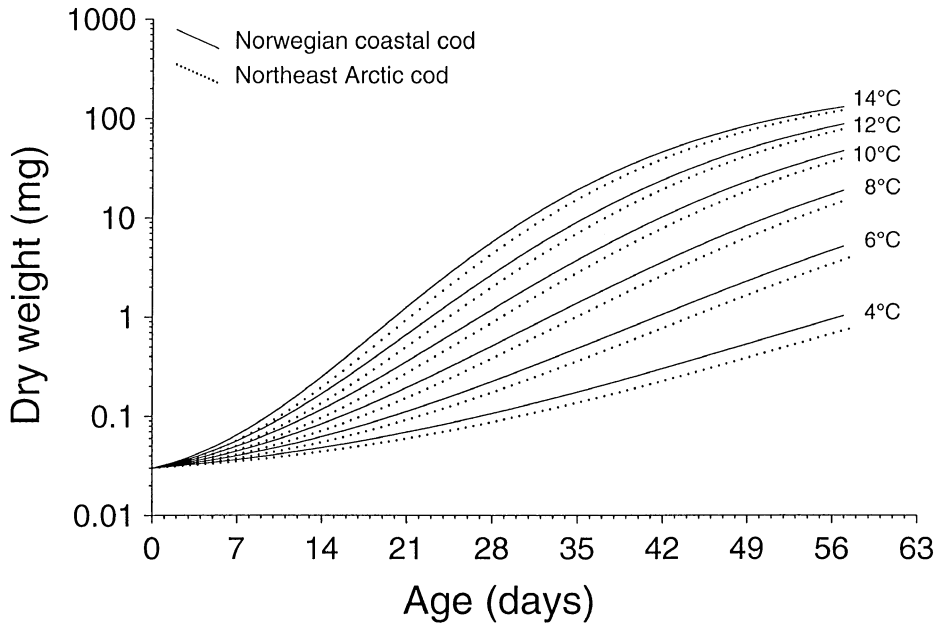
Larval stage-specific mortality *M* was high and variable and ranged from 0.035 to 0.109·day^{-1} for NC and from 0.019 to 0.110·day^{-1} for NA (Table 5). High *M* was observed during three critical periods: the first day after the larvae had been transferred to the rearing tanks, at the onset of first-feeding, and during development and filling of the swim bladder at a larval size of 6–10 mm SL. No immediate increase in *M* was recorded in the viability groups, with survival ranging from 80 to 98% (NC) and from 88 to 100% (NA) on day 7. The *M*/*G* ratio during the larval stage ranged from 0.23 to 0.58 for NC and from 0.19 to 1.12 for NA at the different temperatures. The estimated mean *M*/*G* ratio was <1.0 for both stocks, averaging 0.39 and 0.49 for NC and NA, respectively, showing a net biomass gain (Table 5). Subsequent *M* of fish >12 mm mean SL was negligible and comprised <2.6% of the initial number of larvae in the tank.

Table 2. Summary of the initial values and growth parameters generated by the Gompertz equation (Appendix, eq. A4).

			Parameter estimation				
Stock	DW_0 (mg)	DW_∞ (mg)	*A*	*a*	*b*	*n*	r^2
NC	0.030	250	0.271 (0.030)	0.0065 (0.0006)	0.0044 (0.0001)	1072	0.95
NA	0.030	250	0.198 (0.022)	0.0061 (0.0007)	0.0044 (0.0001)	1020	0.94

Note: The parameters are based on DW measurements of NC and NA larvae and juveniles during their first 8 weeks of life, reared at six constant temperatures in the range of 4–14°C. Initial values DW_0 and DW_∞ are fixed according to the range of the data set. Values in parentheses represent the SE of the estimated parameters.

Fig. 4. Modified Gompertz growth curves of ln DW at age for NC and NA larvae and juveniles reared at six constant temperatures from 4 to 14°C. Equation and parameter estimates are given in the text and Table 2, respectively.



Taking both experiments into account, larval stage specific *M* varied with respect to year, temperature, and stock, without showing any distinctive trends (Table 5).

Discussion

Temperature may be the single most important factor determining the growth rates of early life stages of fish in the field (Houde 1989; Blaxter 1992). The growth rate of cod larvae in this study increased at temperatures from 4 to 14°C (e.g., an increase in temperature from 6 to 12°C generated a 17-fold higher DW after 8 weeks). Successful rearing of cod larvae at 10°C and a positive correlation of *G* with temperature, in the range of 4–10°C, have previously been reported (Laurence 1978). Estimated values of Q_{10} in the range of 3.1–3.5 for *G* of larval cod between 6 and 10°C in our experiment are higher, although still comparable with a value of Q_{10} of 2.5 for larval cod between 7 and 10°C in Laurence (1978).

Estimated T_{opt} for G_{max} of larval cod fed in excess is in the range of 14–16°C. The T_{opt} is high and close to the reported upper lethal temperature, ranging from 15.5 to 18°C, of yolk-sac larvae of cod acclimated to 7–9°C (Yin and Blaxter 1987). Furthermore, the estimated T_{opt} is higher than previously suggested for larvae in the field, 5.9°C (Campana and Hurley 1989), but close to what has been reported for juveniles and larger cod within the size range 250–2000 g, 13.5°C (Jobling 1988). Previous efforts to model age- and temperature-dependent growth in field have been influenced by covarying temperature and food conditions. Restricted prey availability can possibly explain the relatively low temperature estimated for G_{max} of cod larvae in the field given by Campana and Hurley (1989). The term "optimum temperature for growth" therefore should only be used where fish are feeding close to maximum ration (R_{max}), since restricted food intake will have a marked influence on G_{scope} at any given temperature (Brett 1979; Jobling 1994), effectively reducing T_{opt} at lower rations (Brett 1979).

Cod larvae and juveniles demonstrated a dome-shaped relationship between weight-specific growth rate and body size. Growth rate initially increased with larval size at all temperatures, peaked at a premetamorphic size of 0.1–1.0 mg DW, and then declined during the juvenile stage. The estimated G_{max} for both NC and NA larvae exceeded 25%·day^{-1}. These observations are in accordance with some earlier mesocosm and enclosure studies on cod (van der Meeren and Næss 1993; van der Meeren et al. 1994). Average values of *G* in the range of 18.1–22.3%·day^{-1} have been reported for larval cod reared for 46 days in enclosures at sea temperature increasing from 7°C initially to 16°C at termination (van der Meeren et al. 1994). An ontogenetic increase in digestive capacity offset by metabolic cost of growth is further expected to result in a peak or maximum growth potential at a certain body size (van der Meeren

Table 3. Size-at-age (dry weight, mg) of NC and NA larvae and juveniles reared at different temperatures.

Stock	Age (days)	4°C			6°C			8°C			10°C			12°C			14°C		
		Obs	Est	*n*	Obs	Est	*n*	Obs	Est	*n*	Obs	Est	*n*	Obs	Est	*n*	Obs	Est	*n*
NC	7	0.025	**0.037**	34	0.048	**0.040**	14	0.032	**0.044**	24	0.056	0.050	10	0.048	**0.057**	22	0.037	0.065	4
	14	0.036	**0.048**	32	0.098	**0.062**	13	0.081	0.084	21	0.104	0.117	16	0.168	0.169	28	0.151	**0.251**	13
	21	0.054	**0.069**	31	0.217	**0.112**	11	0.164	0.195	37	0.649	**0.357**	17	0.787	0.671	29	0.935	**1.264**	17
	28	0.109	0.107	28	0.452	**0.225**	11	0.516	0.514	40	1.558	1.195	17	3.088	**2.702**	28	3.805	**5.731**	9
	35	0.155	0.176	21	0.883	**0.486**	14	1.738	1.393	15	3.863	3.779	13	5.808	**9.139**	25	12.199	**19.227**	17
	42	0.250	0.303	40	1.682	**1.069**	23	5.972	**3.593**	21	10.388	10.285	22	21.372	24.075	34	48.508	46.335	8
	49	0.503	0.536	42	2.663	**2.307**	19	12.358	**8.374**	26	19.797	23.285	20	39.687	49.593	37	84.936	84.571	11
	56	0.714	**0.956**	53	4.953	4.729	14	22.798	**17.242**	24	36.942	44.043	18	83.611	83.157	36	148.269	125.714	13
NA	7	0.024	**0.035**	19	0.036	0.038	19	0.030	**0.041**	33	0.041	**0.046**	30	0.045	**0.051**	38	0.038	**0.057**	35
	14	0.034	**0.044**	23	0.060	0.055	27	0.069	0.072	36	0.121	0.097	24	0.105	**0.136**	32	0.130	**0.197**	27
	21	0.055	0.060	24	0.161	**0.092**	29	0.094	**0.154**	23	0.515	**0.274**	22	0.571	0.505	31	0.824	0.946	8
	28	0.084	0.088	20	0.244	**0.175**	29	0.289	0.385	17	1.548	**0.886**	23	2.350	2.017	32	3.870	4.365	16
	35	0.095	**0.138**	13	0.604	**0.361**	26	2.472	**1.022**	3	3.600	**2.815**	27	5.822	**7.035**	35	10.093	**15.406**	14
	42	0.146	**0.228**	20	1.255	**0.777**	17	5.458	**2.649**	7	8.615	7.900	18	16.368	19.445	26	30.322	**39.277**	12
	49	0.244	**0.390**	18	1.865	1.668	21	8.852	6.317	4	15.737	18.647	20	39.685	42.075	23	69.302	75.250	9
	56	0.277	**0.682**	7	3.299	3.454	26	21.280	**13.443**	5	31.808	36.281	22	65.011	73.633	24	103.891	116.077	6

Note: Observed (Obs) values are retransformed data. Estimated (Est) values from the modified Gompertz equation (Appendix, eq. A4) presented in boldface differ from the 95% confidence interval.

1993). These results are of particular interest because it is not the mortality rate alone that determines stage-specific survival but rather the *M/G* ratio. An increase in *G* alone can act to impart major reductions in stage-specific mortality rate, *M*/*G*, without concomitant reductions in *M* (Houde 1997*b*). However, the potential for *G* to increase during the larval stage has not been documented for gadid larvae in the field (Houde 1997*b*), although it has previously been described for a few other species, e.g., American shad (*Alosa sapidissima*), striped bass (*Morone saxatilis*), and Pacific herring (*Clupea pallasi*) (Houde 1997*b*). The association of increased *G* with increasing size indicates that better foraging ability is associated with advancing development (Pepin 1991).

Stock-specific differences in mean DW at age were observed, with NC generally growing better than the coreared NA from day 7 onward. A higher *G* among NC (14.4–22.3%·day^{-1}) than among NA larvae (13.6–19.7%·day^{-1}) given identical conditions has previously been reported (van der Meeren et al. 1994) and further documented for juveniles and adult cod of the same origin (Svåsand et al. 1996). Faster somatic growth of the southern NC stock, as compared with NA, through the larval and early juvenile periods did not support the hypothesis of countergradient latitudinal variation in the growth of fishes (Conover et al. 1997). Recently, strong evidence has been provided that the capacity for somatic growth in the juvenile stage of some species, e.g., striped bass, varies genetically among native populations, being inversely correlated with the length of the growing season across a latitudinal gradient (Conover et al. 1997). The observed growth performance of the two cod stocks studied, however, may reflect differences in life history strategy. In nature, although growing slower and mature at an advanced age (Godø and Moksness 1987), NA gains a considerable greater maximum size in length and weight than NC. Furthermore, the growth pattern of the two cod stocks did not reflect any temperature adaptation across latitudes, e.g., high-latitude forms display faster growth at low temperatures, while southern forms grow faster at high temperatures (Lonsdale and Levinton 1985). Except for the occurrence of NC larvae growing better than the NA larvae at 4°C, which is difficult to explain with respect to geographical distribution, the differences in *G* and G_{max} between the two stocks are minor relative to the significance of temperature.

Due to the setup of the spawning tanks, i.e., mixed spawning groups, it was not feasible to relate the larvae to individual spawners. Effects of maternal origin cannot be separated from other genetic stock effects on the basis of the present data. Size and condition factor of the females broodfish are known to influence egg and larval size of cod at hatching (e.g., Blom et al. 1994*a*). Nevertheless, the average growth rates during the larval and early juvenile stages did not differ between progeny of large and small females (Blom et al. 1994*a*).

Weight at length for larvae and juveniles of both stocks increased with temperature, indicating a positive correlation between temperature and condition level. Larvae reared at 12°C were 49% heavier than larvae of similar length at 4°C. The maintenance ration R_{maint} increased with temperature (e.g., Brett 1979) and so did *G* within the temperature range 4–14°C in this study. Food was not a limiting factor; conse-

Fig. 5. Estimated weight-specific growth rate at age for NC and NA larvae and juveniles reared at temperatures from 4 to 14°C. Values for growth rate are estimated from the derivative of the modified Gompertz equation (Appendix, eq. A6).

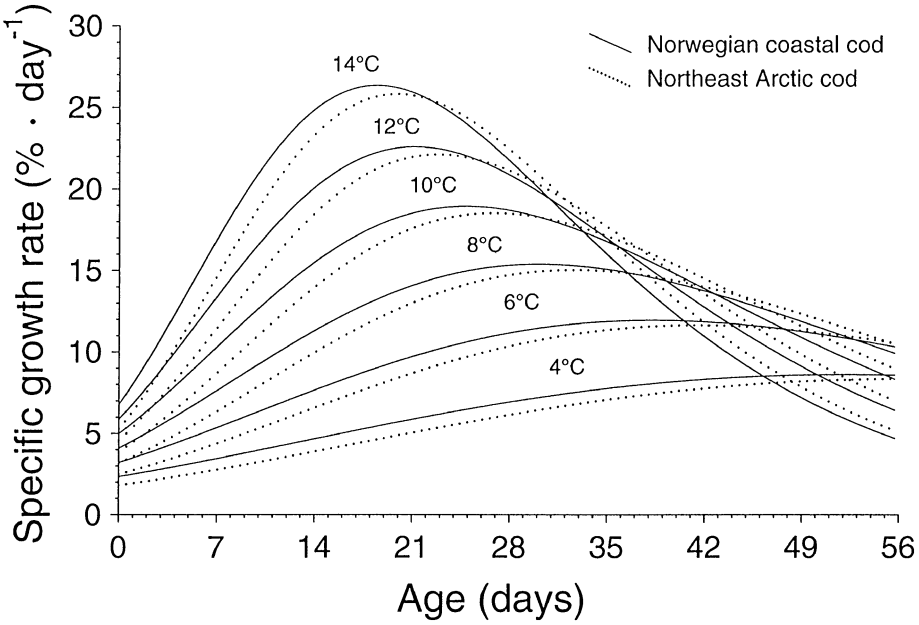
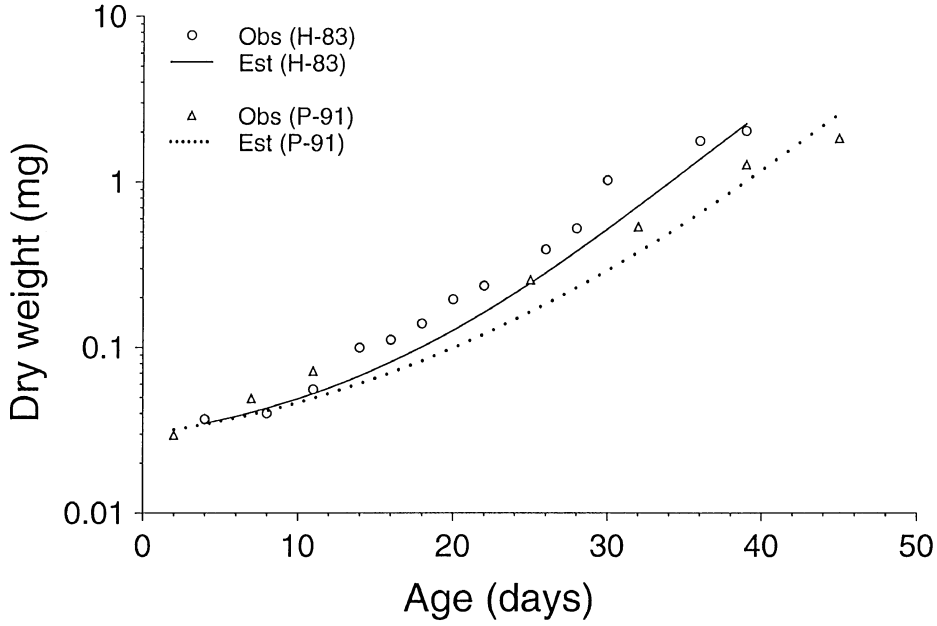


Fig. 6. Current modified Gompertz model for NC, tested with independent growth data of larval cod from two mesocosm studies, Hyltropollen 1983 (H-83) (Folkvord et al. 1994) and Parisvatnet 1991 (P-91) (Blom 1995). Observed (Obs) and estimated (Est) values are presented.



quently, consumption increased with increasing temperature. Larvae and juveniles were not starved or gutted before weighing. Nevertheless, the differences in the condition level of the fish cannot be explained by the difference in weight of the stomach contents alone. Evidence of a stock-specific difference in weight at length was found in early juveniles, with NC being heavier than NA. Differences in body form and energy allocation among juveniles and adults have been documented, with NA having lower condition factor and hepatosomatic indices than NC (Svåsand et al. 1996).

Combining the data across both years, temperature- and stock-dependent growth of larval and early juvenile cod was well described by Gompertz growth curves. The Gompertz model is suitable when an inflection in the growth trajectory is evident (Zweifel and Lasker 1976) and has previously been employed to predict larval growth of fish, e.g., cod (Bolz and Lough 1988). The Gompertz curve is asymmetrical about the inflection point and approaches the asymptote more gradually than the symmetrical logistic curve (Kaufmann 1981) and more resembles the growth pattern of the early life stages of cod. However, to generalize the model, the parameter α had to be substituted with a temperature

Fig. 7. Length–weight relationships of NC and NA. Generalized common equations for larvae (larv) of overlapping size (SL ≤ 10 mm; temperatures 4, 6, 8, 10, 12, and 14°C) and early juveniles (juv) (SL ≥ 14 mm; temperatures 10, 12, and 14°C) are presented.

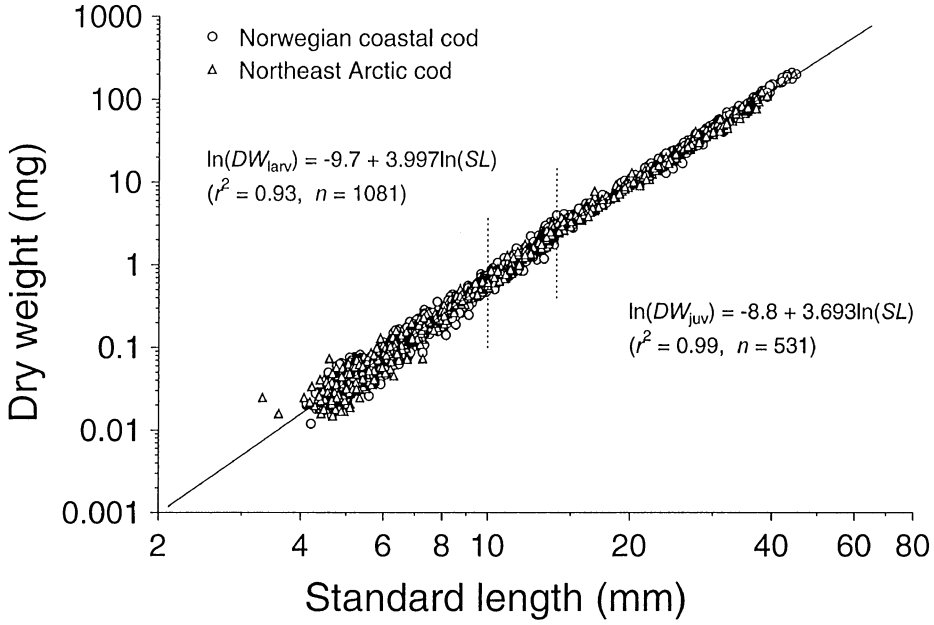


Table 4. Length–weight relationships of NC and NA larvae and juveniles of overlapping size ranges.

Stage	Stock	Temperature (°C)	Range in length (mm)	Median length (mm)	Intercept (*a*)	Slope (*b*)	*n*
Larvae	NC	4	4.1–10.0	6.5	–9.85	4.01	228
	NC	6	4.6–10.0	6.7	–9.60	4.01	53
	NC	8	4.5–9.8	6.3	–9.32	3.76	96
	NC	10	4.6–9.9	6.6	–9.52	4.01	38
	NC	12	4.4–9.9	6.4	–9.45	4.01	60
	NC	14	4.7–9.9	7.0	–9.57	4.01	21
	NA	4	4.4–10.0	5.9	–10.07	4.14	142
	NA	6	4.3–10.0	6.9	–10.00	4.14	121
	NA	8	3.3–9.6	5.4	–8.52	3.33	100
	NA	10	4.5–10.0	6.1	–9.92	4.14	72
	NA	12	4.4–10.0	5.5	–9.83	4.14	87
	NA	14	4.6–8.5	5.3	–9.97	4.14	63
Juveniles	NC	10	14.5–35.0	23.3	–8.71	3.66	71
	NC	12	14.0–40.0	26.5	–8.63	3.66	148
	NC	14	14.3–45.0	29.8	–8.58	3.66	56
	NA	10	14.0–34.5	21.4	–8.71	3.66	82
	NA	12	14.2–39.0	22.8	–8.68	3.66	120
	NA	14	14.1–44.5	23.8	–8.66	3.66	54

Note: Parameters of the general allometric model (eq. 6) were estimated and the number of observations (*n*) is provided. Data from replicates are combined. Larvae reared at 8°C significantly differed in slope from the other groups and separate stock specific regressions were computed for this treatment.

function. Furthermore, in order to track growth correctly and avoid serious over- or underestimations, the model was restricted to the range of the data set by defining fixed initial and "infinite" values.

If the temperature increases, the temperature term (eq. 8) will push the Gompertz to its asymptote more quickly, but compared with the model of Campana and Hurley (1989), the expression will not produce a temperature optimum for growth. This is an unrealistic feature, which limits the application of the models to temperatures below the optimum. However, the T_{opt} for G_{max} of both stocks fed in excess was beyond the temperature range studied. Yet, the data basis for a more complex model, including a temperature optimum, does not exist. Further effort should be directed towards construction of growth–ration curves for a broad range of temperatures, simulating restricted food conditions. The previous

Table 5. Summary of mean daily mortality rates (*M*) and ratios of mortality rates to mean daily specific growth rates (*M*/*G*) during the larval stage (DW ≈ 1.3 mg), estimated mean final survival (*S*, %) until age 56 days, and number of days to complete larval mortality (CM) in the respective viability groups.

Stock	Temperature (°C)	*M*	*M*/*G*	*S*	CM
NC	4[a]	0.037	0.53	14.5	19
NC	6	0.035	0.34	25.3	22
NC	8[b]	0.058	0.41	8.7	16
NC	10	0.043	0.26	31.8	16
NC	12	0.043	0.23	35.5	13
NC	14[b]	0.109	0.58	13.6	12
NA	4[a]	0.053	1.12	6.1	29
NA	6	0.019	0.19	45.0	24
NA	8[b]	0.077	0.58	4.9	17
NA	10	0.033	0.21	39.1	16
NA	12	0.052	0.29	26.5	14
NA	14[b]	0.110	0.56	11.0	13

Note: Estimated values of *M* and *M*/*G* of larvae at 8°C are based on one tank.

[a]Estimated values of larvae age 56 days, DW < 1.3 mg.

[b]Reduced final survival due to one tank being terminated before the experiment ended.

model of Campana and Hurley (1989) was developed for cod and haddock (*Melanogrammus aeglefinus*) grown at varying ambient temperature. Although the present growth models are based on larvae reared under constant temperature conditions, it is possible to integrate growth across a time-varying temperature regime using DW at a given temperature to estimate the corresponding age in days under an alternative temperature regime.

Finally, the predictive capability of the model for the NC stock was assessed through tests with independent growth data of larval cod from two mesocosm studies (Folkvord et al. 1994; Blom 1995). The model slightly underestimated the growth for larvae <1.5 mg DW. Size-dependent mortality or cannibalism occurring in the mesocosms could have resulted in the predicted growth anomalies. Ambient temperature may also differ from the mean daily estimated temperature actually used in the model. The high growth rates obtained in both mesocosms, however, are reflected by the high larval survival (ranging from 25 to 40% to metamorphosis) in these studies (Blom et al. 1994*a*; Folkvord et al. 1994).

From a multispecies perspective, mortality rates and growth rates are highly correlated in the field (Houde 1989; Pepin 1991), with rates often inversely related for single species (e.g., Campana et al. 1989). If mortality rates are specific to particular life periods, then estimating the duration and rates that apply within the period is crucial (Chambers and Leggett 1987). Given that metamorphosis in larval fish tends to be size rather than age related (Chambers and Leggett 1987), the duration of the larval stage or age at metamorphosis declines rapidly as growth rate increases. Larval cod reared at 14°C reached the onset of metamorphosis after 23 days compared with more than 56 days for fish at 4°C. An inverse relationship between stage duration and temperature has been well documented in other species (Laurence 1975). Time to metamorphosis of the winter flounder (*Pleuronectes americanus*, previously *Pseudopleuronectes americanus*) was 49 days at 8°C and 80 days at 5°C (Laurence 1975). According to the "stage duration" mechanism, if juveniles experience a lower mortality rate than larvae, then individuals that develop faster and metamorphose at an earlier age would have a lower probability of mortality compared with individuals that remain longer as larvae (Chambers and Leggett 1987; Hare and Cowen 1997). Recent studies support the hypothesis that fast growth increases the survival of cod during the larval (Meekan and Fortier 1996) and juvenile (Campana 1996) stages.

Mortality rates during the early life stages of fish are generally high (e.g., McGurk 1986). High mortality observed during the first day after the yolk-sac larvae had been transferred to the rearing tanks may partly be explained by stress during handling or as a consequence of variable larval quality or viability. Furthermore, mortality seems to be associated with two more critical periods, larvae that failed to initiate and maintain successful feeding in switching from endogenous to exogenous nutrition and, later, larvae in the size range of 6–10 mm SL that were unable to regulate and fill their swim bladder. This mortality pattern is typical of marine fish larvae and has previously been reported for intensively reared cod larvae (Howell 1984). Cod larvae, in contrast with Atlantic herring (*Clupea harengus*) larvae, appear to be particularly vulnerable to nitrogen supersaturation. Mortality of fish >12 mm mean SL was negligible in the present experiments.

In summary, this study has demonstrated a maximum weight-specific growth potential for larval cod exceeding 25%·day^{-1}. The estimated temperature optima for maximum growth of 14.2 and 16.2°C for larval NA and NC, respectively, fed in excess are higher than previously suggested. Overall, a positive correlation between temperature and condition level was found. The growth rate is markedly size dependent, describing a dome-shaped relationship in both stocks. Growth curves of size at age are well described by a generalized Gompertz model. A stock-specific difference in mean DW at age was observed, with NC growing better than NA. However, neither temperature adaptation across latitudes nor countergradient latitudinal variation in growth capacity of the two larval cod stocks was indicated.

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Appendix

Initiation, reparameterization, and final equations for the modified Gompertz model are as follows. The initial DW_0 and "infinite" DW_∞ values were fixed according to the range of the data set, $DW_0 = 0.030$ mg and $DW_\infty = 250$ mg, respectively:

(A1) $\ln DW_0 = C + A$

and

(A2) $\ln DW_\infty = C + Ae^K$.

Substituting eq. A1 into eq. A2, an equation for parameter K is derived:

(A3) $$K = \ln\left(\frac{\ln DW_\infty - \ln DW_0 + A}{A}\right)$$

and

(A4) $$\ln DW(t) = \ln DW_0 - A + A\left(\frac{\ln DW_\infty - \ln DW_0 + A}{A}\right)^{(1-e^{-(a+bT)t})}.$$

Data were fitted to eq. A4 and the model tracks growth for the first 8 weeks of life. Furthermore, the instantaneous growth coefficient g is expressed as the first derivative of eq. 7:

(A5) $$g = Ae^{K(1-e^{-\alpha t})}\alpha K e^{-\alpha t}$$

or reparameterized with respect to $\ln DW_\infty$ and $\ln DW_0$:

(A6) $$g = \left[A\left(\frac{\ln DW_\infty - \ln DW_0 + A}{A}\right)^{(1-e^{-(a+bT)t})}\right]\left[(a+bT)\ln\left(\frac{\ln DW_\infty - \ln DW_0 + A}{A}\right)e^{-(a+bT)t}\right].$$