

Growth of North-east Arctic cod (*Gadus morhua* L.) in relation to ambient temperature

K. Michalsen, G. Ottersen, and O. Nakken



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Temperature related changes in horizontal distribution of North-east Arctic cod are described and the influence of temperature on the growth is interpreted. By using data from acoustic and bottom trawl surveys in the Barents Sea conducted in February 1988–1995, mean length at age is related to the winter temperature. Mean lengths at age increased with increasing temperature for cod of age 2–6. Mean individual growth was highest for year classes experiencing high temperatures. Due to the seasonal migration patterns of cod, the actual annual means of ambient temperature as well as the differences between these means are lower than the values from February alone, used in this study. Thus, by using the ambient winter temperature instead of annual mean values the effect temperature has on growth is probably underestimated. Increased abundance of young cod is associated with an extension of the distribution area towards east and north into colder water. Even though the individual consumption of capelin by cod increased in these years, the increase in abundance was accompanied by reduced growth. Hence a growth–temperature relation may wrongly be interpreted as a growth–density (abundance) dependency if ambient temperature is not included in the analysis.

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Kathrine Michalsen, Geir Ottersen, and Odd Nakken: Institute of Marine Research, PO Box 1870 Nordnes, N-5024 Bergen, Norway. Correspondence to K. Michalsen: tel: +47 55 238500; fax: +47 55 238387; e-mail: katherine@imr.no

Introduction

Although growth of fishes is dependent on the availability of prey, quantitatively as well as qualitatively, growth is also the integration of a series of processes (feeding, assimilation, metabolism, transformation, and excretion) where rates are all controlled by temperature (Brett, 1979; Wootton, 1990; Clarke, 1993; Jobling, 1994). In addition temperature affects almost all species in the ecosystem, making it an important indicator of changes in fish population dynamics (Daan, 1994).

For the North-east Arctic cod year-to-year changes in growth have been observed over a long period of time (Jakobsson, 1992; Nakken, 1994). An inverse relation between growth and stock abundance has been taken as evidence of density-dependent growth (Ponomarenko, 1967; Nilssen *et al.*, 1994). Additionally, other authors have observed larger mean lengths-at-age at high temperatures as compared to lower ones, and proposed a

positive relation between temperature and growth (Nakken and Raknes, 1987; Loeng, 1989; Jørgensen 1992). Brander (1995) studied 17 North Atlantic cod stocks including North-east Arctic cod and found that most of the observed variability in growth could be attributed to variation in temperature. One of his conclusions was: “In order to evaluate the effect of temperature on population growth it will be necessary to determine precisely the age range over which temperature affects individual growth”. As Brander’s statement indicates, our understanding of the factors controlling growth rates, how these factors interact, and the magnitude of their influence is still incomplete. In many studies of the effects of temperature on fish distribution and population parameters, the temperatures at fixed stations or sections are used. Ottersen *et al.* (1998) found that these temperatures do not reflect the interannual variability in temperature experienced by the cod, and suggested that it is the temperature in the actual surroundings of the fish, the ambient temperature, that

Table 1. Number of stations used for each year and age group, 1988–1995. Total is total number of stations at which the age group occurred. “>100” is number of stations with densities above 100 specimens per square nautical mile.

Age	1988		1989		1990		1991		1992		1993		1994		1995	
	Total	>100														
1	95	2	230	61	273	168	302	208	302	223	311	205	345	320	383	361
2	243	99	230	85	271	134	302	217	302	227	311	228	345	275	383	259
3	274	133	230	113	265	130	278	154	300	258	311	267	345	252	383	273
4	274	142	230	160	265	142	278	131	300	243	311	272	345	269	383	249
5	274	154	230	152	265	151	278	132	300	167	311	239	345	258	320	239
6	274	82	230	165	265	110	278	131	300	134	311	132	345	227	304	230
7	274	22	230	72	265	118	278	85	300	89	311	59	345	87	304	166

should be used in further studies concerning temperature effects on fish.

In the present study, temperature related changes in geographical distribution of North-east Arctic cod are described and the influence of ambient winter temperature on the distribution of length at age of the fish is interpreted. Ambient winter temperatures, estimated by Ottersen *et al.* (1998) are used in the analysis. We also estimate the annual growth rate for some year classes and relate it to the winter temperature experienced during particular years as well as to the temperature accumulated during their lifetime.

Material and methods

The material

The data used in this study originate from combined bottom trawl and acoustic surveys in the Barents Sea in February each year from 1988 to 1995. The main purpose of these surveys, which are a part of a longer time series, is to establish estimates or indices of abundance at age (swept area-based as well as acoustic estimates) of cod and other demersal species. Jakobsen *et al.* (1997) have given a comprehensive review of the whole survey period 1981–1997 and discussed the effects on the results of changes and improvements in survey design, sampling intensity, and techniques which have taken place.

Prior to 1993 swept area indices were computed for a standard area, ABCD (see Jakobsen *et al.*, 1997). However, for most of those years the acoustic surveys covered a somewhat wider area where a number of bottom trawl stations were carried out in order to identify the acoustic scatterers. Also, within the standard area some bottom trawl hauls (and pelagic hauls) were made for the same purpose. Thus the actual number of bottom trawl catches sampled during each survey was higher than that used for swept area computations of abundance (Jakobsen *et al.*, 1997, Table 1). Since 1993 the area for which swept area indices have been computed corresponds to the total survey area, which was expanded that year towards north and east.

In order to utilize the information from the entire area surveyed and sampled, we have each year included all bottom trawl stations in the present investigations; both those taken in predetermined positions and those carried out for the identification of acoustic scatterers. We did omit densities at age less than 100 fish per square nautical mile from the calculations of mean length at age. For small fish of 15–20 cm in length (1 and 2-year-olds), this density corresponded to a catch of about three or less fish. On the other hand, this corresponded to a catch of one fish for those greater than 50 cm. Inspection of the spatial distribution of mean length-at-age for each age and year did not indicate that this procedure would introduce patterns into the data.

In the bottom trawl surveys a Campelen 1800 shrimp trawl was used. Further specifications on equipment and methods are given in Jakobsen *et al.* (1997). Swept area density estimates (number of fish per square nautical mile, ρ) were calculated for each 5 cm length group at each trawl station as in Ottersen *et al.* (1998). At selected trawl stations otoliths from two fish at each 5 cm length interval were collected and the age read, giving an age/length key for each of five different sub-areas. This key is only based on stations within the standard area and without stations carried out to identify acoustic scatterers. Densities at length at each station were converted to densities at age by applying the appropriate age/length keys. Figure 1 shows the distribution of density estimates and bottom temperature at trawl stations for 3 and 5-year-old cod in 1990 and 1994.

Estimates

Mean lengths at age for each station (s), each temperature interval (int) and the whole survey area were estimated for each year as follows:

$$\text{Station: } L_{a,s} = \sum_i L_{a,s,i} * \rho_{a,s,i} / \sum_i \rho_{a,s,i} \quad (1)$$

where the summation is for length groups (i) and $\sum_i \rho_{a,s,i} = \rho_{a,s}$ is the density of fish of age a at station s.

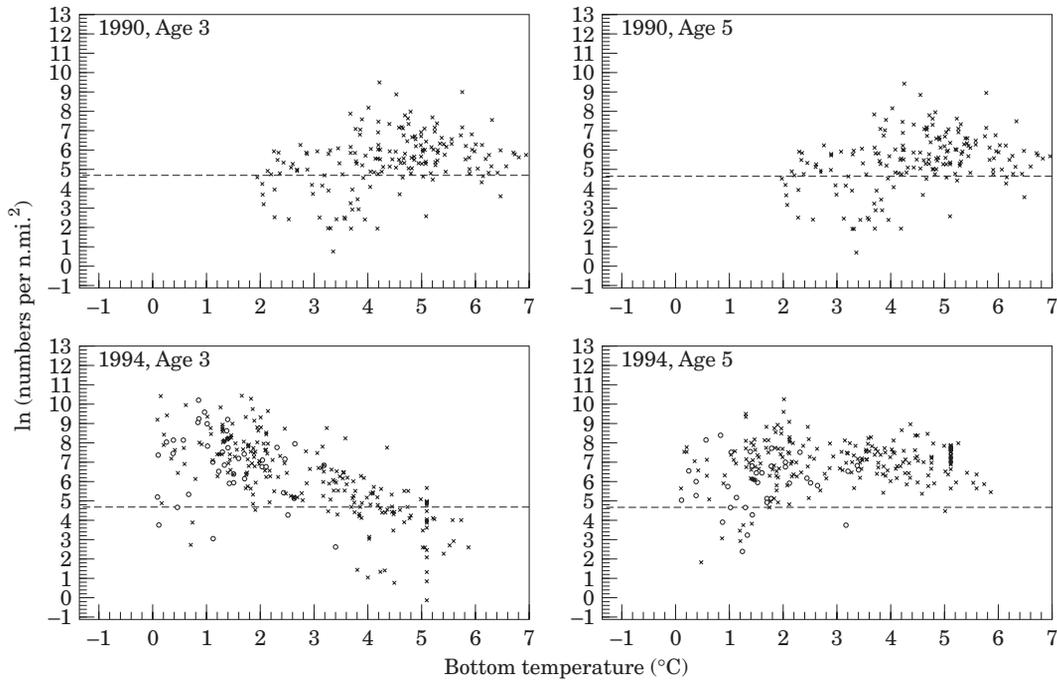


Figure 1. The distribution of density estimates at stations (natural logarithm of numbers per square nautical mile) for the 3 and 5-year-old cod in 1990 and 1994, within temperature intervals. Open circles represent stations outside the standard area ABCD, while dotted lines indicate a density of 100 fish per square nautical mile.

$$\text{Temperature interval: } L_{a,int} = \frac{\sum_s L_{a,s,int} \cdot \rho_{a,s,int}}{\sum_s \rho_{a,s,int}} \quad (2)$$

where $\rho_{a,s,int} / \sum_s \rho_{a,s,int}$ is the weighting factor and the summation is for stations (s) within the temperature interval (int). Note that $\sum_s \rho_{a,s,int} / \sum_s = \rho_{a,int}$ is the average density of fish of age a within that temperature interval.

$$\text{Whole survey: } L_a = \frac{\sum_s L_{a,s} \cdot \rho_{a,s}}{\sum_s \rho_{a,s}} \quad (3)$$

where the summation is for all stations in the survey within each age group.

Mean weights at age were taken from ICES (1996) and used to calculate growth rate. Stock numbers at age for the time series were taken from ICES (1996). Estimates of the temperature of the water masses actually surrounding the fish, the ambient temperature, were taken from Ottersen *et al.* (1998). An average density at age (number per square nautical mile) was computed for each 0.5°C temperature interval (T_{int}) and multiplied by the area of the interval in order to arrive at numbers at age at temperature intervals. These numbers were used as weights in the calculation of the mean ambient winter temperature for each age group and year, \bar{T}_{amb} . Two estimates of mean ambient winter temperature for each age and year are used in this study. These estimates were computed by combining each of the two types of density estimates (acoustic and swept area) with the temperature

at the bottom (Ottersen *et al.*, 1998). Maps comparing bottom temperature and mean lengths at age as well as densities at age at trawl stations were examined for all years of investigation, and the ones from 1994, showing bottom temperatures and length at age for age groups 3 and 5 are presented.

Analyses

Geographical variation in mean length at age

Inspection of each year's distribution map in mean length at age indicated that length at age as a rule decreased from west to east. In order to quantify these geographical deviations, differences in mean length at age in western and eastern areas, south of 73°N for each year were analysed by using the following expression:

$$\Delta L_a = L_a (\text{West of } 20^\circ\text{E}) - L_a (\text{East of } 35^\circ\text{E}) \quad (4)$$

where the mean values were obtained by applying Equation (2) for each of the two areas.

Distribution of mean length at age and temperature

In an attempt to quantify the within year relation of length at age on temperature a linear regression analysis was carried out as:

$$L_a = \text{intercept} + \text{slope} * T_{\text{int}} \tag{5}$$

using corresponding values of $L_{a,\text{int}}$ and T_{int} as input. The regression was done for each year separately as well as for all years combined.

We are mainly interested in the slope values in the above equation, i.e. the variation in length at age with temperature. A linear regression for all years combined may result in a biased slope depending on the range in temperature and/or length the various years. Two years can have equal slopes but different intercepts. If data, in one year, is available for only a part of the total combined range, pooling of the two data sets into one regression will result in a slope different from the common value obtained with the two sets kept separate. To avoid such a bias and to investigate the magnitude of the possible bias introduced by the procedure used above, we computed an overall slope as the weighted mean of each year's slope using the inverse of the standard error as weight;

$$\text{Weighted slope} = \left(\sum_{i=1988}^{1995} \text{slope}_i * \frac{1}{SE_i} \right) / \sum_{i=1988}^{1995} \frac{1}{SE_i} \tag{6}$$

Growth and mean ambient temperature

The effects of ambient temperature on growth were investigated using two approaches: First, absolute and instantaneous annual growth rates arrived at from annual increments in length and weight were compared with the corresponding mean ambient temperatures. Second, mean annual growth rates over lifetime (length at age) of each year class were compared with the corresponding lifetime temperatures by accumulating mean ambient temperatures over age.

The absolute growth rate at age (a) was defined as the length or weight increment during one calendar year:

$$G_a (\text{length}) = (L_{a+1} - L_a) \tag{7}$$

and

$$G_a (\text{weight}) = (W_{a+1} - W_a). \tag{8}$$

The instantaneous annual growth rate was calculated as:

$$g_a (\text{length}) = (\ln L_{a+1} - \ln L_a) \tag{9}$$

and

$$g_a (\text{weight}) = (\ln W_{a+1} - \ln W_a) \tag{10}$$

where L_a (W_a) and L_{a+1} (W_{a+1}) are the lengths (weights) of the same year class when of age a and a + 1, respectively.

Linear regression analyses of mean lengths at age (L_a) on corresponding lifetime temperatures were performed by using both swept area based and acoustically based mean ambient temperatures in the regressions.

$$L_a = \text{intercept} + \text{slope} * \sum_{i=1}^a \bar{T}_{\text{amb},i} \tag{11}$$

where the summation of \bar{T}_{amb} gives the lifetime ambient temperature at age a, for each year class. Equation (11) is convenient for studying how the temperature effect on growth varies with the age of the fish. The slope in the equation represents the change in mean length at age with temperature. Positive slope values indicate that length at age, i.e. lifetime growth, increases with increasing lifetime temperature. Further, when two successive age groups have equal slopes (parallel lines) it means that the length increment from the younger to the older age is the same regardless of temperature and hence that this increment is not effected by temperature. Therefore a simple comparison of the estimated slopes for each age will yield information on up to what age ambient temperature has had an effect on growth. The slope values for each age represent the increase in length with one degree increase in temperature and can be expressed in relative terms as percent of the mean length at age (L_a).

$$\text{Relative length increment } (^\circ\text{C}^{-1}) = \frac{\text{slope}}{L_a} * 100. \tag{12}$$

When weight is assumed to be related to length by, $W = \text{const.} * L^3$, the relative increase in weight can be estimated as:

$$\text{Relative weight increment } (^\circ\text{C}^{-1}) = 3 * (\text{Relative length increment}). \tag{13}$$

In order to establish a relationship between mean length at age and mean ambient temperature (acoustical), based on as much information as possible, data from Nakken and Raknes (1987) were included in the analysis. For the 3 years 1985–1987, length at age data were taken from ICES (1996), while estimates of mean ambient temperature were calculated by linear regression analyses between existing acoustically based mean ambient temperatures (\bar{T}_{amb} , 1978–1995) and monthly 0–200 m depth sea temperature averages from the Kola section (T_K , Tereschenko, 1996).

Mean ambient temperature and abundance

In earlier works (Shevelev *et al.*, 1987; Ottersen *et al.*, 1998) it is noted that there is a connection between east- and northward distribution of young cod and its abundance. In periods with a general increase in population size the easterly range is extended resulting in low

ambient temperatures. In order to examine this feature we carried out a linear regression of the temperature difference between Kola (T_K) and acoustical based mean ambient temperature [$\bar{T}(3)_{amb}$] for 3-year-olds, on the stock number (N) of 3+4+5-year-old cod, which are the age groups that have the most extensive ecological overlap:

$$T_K - \bar{T}(3)_{amb} = \text{intercept} + \text{slope} * \text{number of fish} \quad (3+4+5) \quad (14)$$

and

$$\bar{T}_{amb} = T_K - [\text{intercept} + \text{slope} * \text{number of fish} \quad (3+4+5)] \quad (15)$$

where Equation (15) expresses the dependency of mean ambient temperature on the thermal regime in the Barents Sea (T_K) as well as on fish abundance.

Results

Geographical distribution of length at age and temperature

In order to illustrate the distribution of length at age and temperature we have selected maps of bottom temperature and mean lengths at trawl stations for 3 and 5-year-old cod in 1994 (Fig. 2). The main tendency is that the temperatures in the Barents Sea always decrease 5–6°C from west to east, regardless of whether it is a cold or warm year. For both age groups shown in Figure 2 the iso-lines showing length have the same general patterns as the isotherms; length decreasing with decreasing temperature. A significant change in length seem to occur when passing the area of the 3 degree isotherm from west to east, with considerable smaller fish in the areas east of that isotherm. Differences in length-at-age between the western (warm) and eastern (cold) part of the area, south of 73°N are summarized in Table 2. Positive values, indicating bigger fish in the western area, were found in all years, for age groups 3–5, except for age 3 in 1989, age 4 in 1991, and age 5 in 1991 and 1993. The greatest differences in length for age group 3–7 were observed in 1994.

The relationship between mean length at age and temperature

Table 3 shows the results of linear regressions of length-at-age on temperature for all years (1988–1995). Although a considerable variation appears, slope values for 2–6 year old fish indicate a positive relation between length-at-age and temperature. The higher the temperature the larger are the fish at age. For cod of age

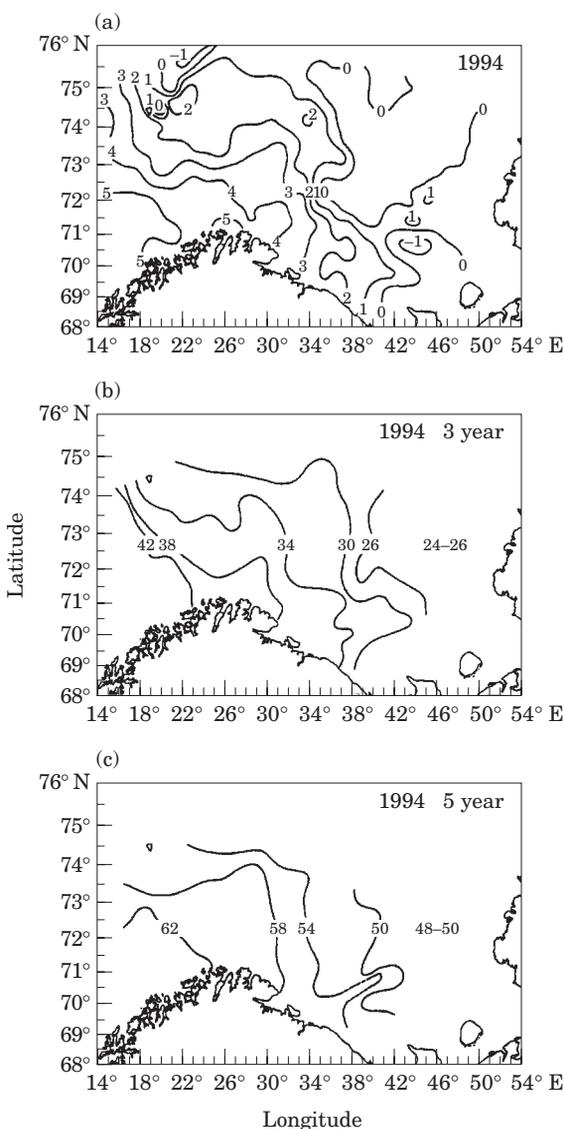


Figure 2. Horizontal distribution of temperature (T °C) at bottom and mean length at age (cm) of 3 and 5-year-old cod in 1994. (a) Isolines for bottom temperature. (b) and (c) Calculated mean length at age at trawl stations for 3 and 5-year-old cod, respectively.

3–5 years, variation in temperature explains 80–96% of the variation in mean length. On the other hand no such relation was found for age groups 1 and 7 having negative or near zero slope values. In Figure 3 the estimated mean lengths at age within each temperature interval, combined for the 8 years of observation, are shown together with the two estimates of slope values from Table 3. This figure emphasizes the tendency towards bigger fish in warmer waters. However the slopes of the full drawn lines representing the results from linear regressions using data for all years

Table 2. Differences in mean length at age (cm) in western and eastern parts of the investigated area, South of 73°N, 1988–1995. [L(West of 20°E) – L(East of 35°E)]. (nfw) indicates years without fish in the western area and (nfe) without fish in the eastern area, while (nfw) indicates years without fish in any of these two areas.

Age	1988	1989	1990	1991	1992	1993	1994	1995	Total*
1	nfw	nfw	nfw	-1.15	-0.73	0.38	0.23	-1.51	-0.56
2	nfw	-1.35	3.39	0.47	-0.48	4.83	-1.32	-0.12	0.78
3	5.73	-0.51	6.20	9.80	4.99	3.75	7.30	2.48	4.97
4	nfe	1.99	1.85	-1.07	3.43	2.58	4.80	3.13	2.39
5	nfe	3.59	nfe	-2.27	1.16	-0.70	10.23	3.92	2.66
6	nfe	6.83	nfe	-0.09	1.41	0.91	9.40	3.83	3.71
7	nfe	nfe	nfe	2.38	-0.51	-2.42	11.76	-2.07	1.83

*Mean difference for all years, 1988–1995.

Table 3. Results of linear regression of mean length at age (L_{int}) on ambient temperature (T_{int}) based on swept area densities, [$L_{int} = \text{intercept} + \text{slope} * T_{int}$] all data 1988–1995. s.e. is standard error, R^2 is the determination coefficient. "Mean" indicates values when all data are combined. Range indicates highest and lowest value from regression from each year.

Age (years)	Intercept (cm °C ⁻¹)		Slope (cm °C ⁻¹)			R ²	
	"Mean" ± s.e.	Range	"Mean" ± s.e.	Range	Weighted	"Mean"	Range
1	12.7 ± 0.2	12.1–13.9	-0.05 ± 0.04	-0.14–0.08	-0.02	0.09	0.08–0.38
2	19.3 ± 0.8	18.3–27.3	1.06 ± 0.20	-0.50–1.99	0.26	0.64	0.26–0.53
3	28.6 ± 0.4	25.0–39.6	1.93 ± 1.10	-0.10–1.97	1.00	0.96	0.05–0.90
4	42.4 ± 0.4	35.7–48.5	0.99 ± 1.10	-0.17–1.22	0.57	0.88	0.13–0.86
5	50.6 ± 0.5	44.1–59.7	0.84 ± 0.11	-0.15–1.96	0.52	0.80	0.02–0.90
6	59.1 ± 0.4	52.5–71.4	0.65 ± 0.10	-0.77–1.59	0.36	0.88	0.13–0.86
7	74.6 ± 0.8	67.9–78.6	-0.50 ± 0.18	-0.58–0.94	0.04	0.42	0.01–0.40

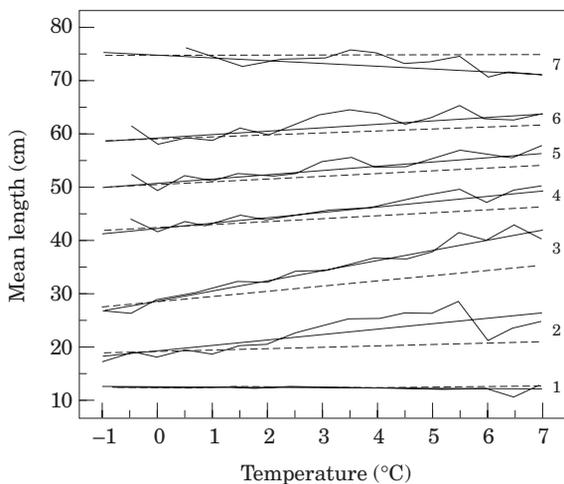


Figure 3. Relationships of length at age and temperature (swept area density) for each age group. Straight full lines are based on results from linear regressions when data from all years were combined, while broken lines are based on weighted means of statistics from regressions for each particular year. Curves represent estimated mean length at age within each temperature interval. Numbers to the right indicate age group.

combined, may be overestimated (see Material and methods). A weighted mean of all years slopes for each age resulted in considerable lower values for ages 2–6. For 3 year old fish the results show an average length dependency of 1.9 cm per °C. This indicates that 3 year old specimens in the warm south-western parts of the area regularly are 9–11 cm longer than those in the cold north-eastern parts.

Growth and mean ambient temperature

Figure 4 shows the annual length- and weight increments of each age group during the period of observation (note that the increments from age a to age $a+1$ are taken from February to February and plotted in the middle of the calendar year the fish was aged a). Growth (in length and weight) increased during the late 1980s reaching a maximum in 1989–1990 for all age groups. From 1990 and onwards growth decreased for all age groups reaching a minimum in 1993. The annual length increment is approximately the same for all age groups, except for the 2-year-olds in 1991.

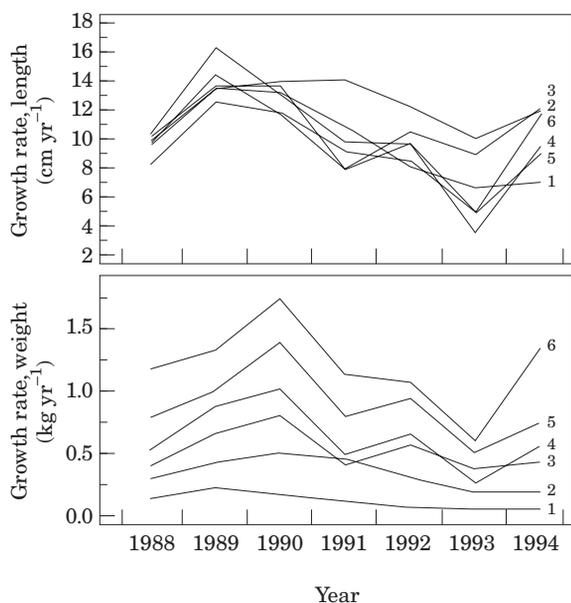


Figure 4. Absolute annual growth rate in length ($L_{a+1} - L_a$, cm) and weight ($W_{a+1} - W_a$, kg). Numbers to the right indicate age group.

Instantaneous annual growth rates in length and weight are presented in Figure 5 and the mean ambient temperature for each age group is given for comparison. The general patterns are similar to those seen in Figure 4 except that there is no delay between growth in weight and length anymore. Due to the seasonal changes in temperature, the temperatures measured in February should be representative for the whole winter situation (November to March), indicating that the temperature that should be compared with the growth increments is the one in the beginning of the following year, as plotted in our graph. When comparing the graphs in Figure 5 the main impression is that the reduction in growth coincided with a decrease in ambient temperature.

Mean lengths at age of each year class are plotted against lifetime ambient temperatures (accumulated over the lifetime of each year class) for the two estimates of ambient temperature and a line is drawn for each of the seven age groups studied (Fig. 6). Both plots indicate the same tendency; a rather pronounced increase in mean length with temperature for ages 2–5. The mean length of age 1 does not seem to be related to temperature and for fish older than 5 years the material is scanty. The positive relation between length and temperature appears to decrease with age from age 2. Linear regressions between mean length at age and accumulated mean ambient temperature based on swept area density and bottom temperature (Table 4a) yield a slope of 2.5 cm per °C for age group 2, which corresponds to a relative increase of 11% in length per °C (33% in weight

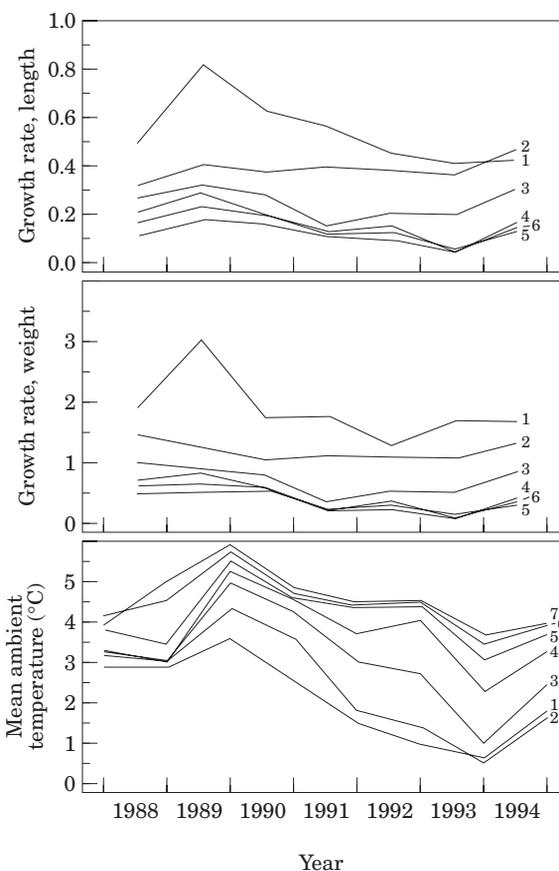


Figure 5. Instantaneous annual growth rates in length ($\ln L_{a+1}/\ln L_a$) and weight ($\ln W_{a+1}/\ln W_a$) compared with mean ambient temperature (swept area density). Numbers to the right indicate age group. Note that growth from age a to age $a+1$ are taken from February one year to February next year and plotted in the middle of the year the fish was aged a .

increments). Based on acoustic density and bottom temperature the slope values are reduced to 1.7 cm and 7% in relative length increments per °C (21% in weight increments, Table 4b).

When data back to 1978 were included (Table 4c, Fig. 7), the length dependency on temperature is reduced, with length increments of 1.2 cm per °C for age group 2. The results also indicate that after age 2 the effects of temperature on growth are small or negligible as illustrated by the almost parallel lines/slightly decreasing slopes for those age groups in Figure 7 and Table 4c. The length increments the fish have gained up to age 2 from higher ambient temperature are maintained at older ages but no additional increments with temperature can be observed. The asterisks in Figure 7, which indicate the length of cod experiencing water temperatures of 4°C throughout their whole life, are in the upper part of the temperature range for all age groups.

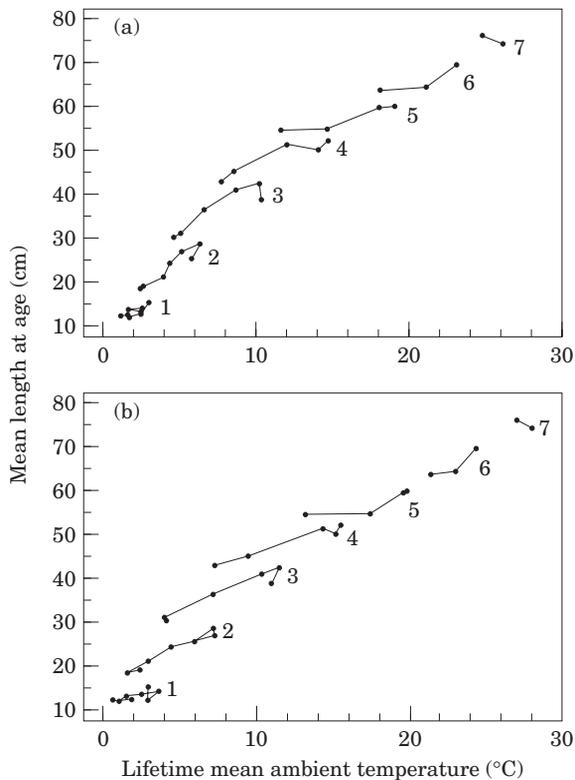


Figure 6. Mean length at age in relation to lifetime mean ambient temperature for (a) swept area density and bottom temperature and (b) acoustic density and bottom temperature. Numbers to the right indicate age group.

Mean ambient temperature and abundance

The linear regression of the temperature difference between Kola and mean ambient temperature for 3 year olds on the stock number of 3+4+5 year olds (Fig. 8), shows a quite strong correlation ($r^2=0.85$). The difference in temperature increases with increasing stock abundance, high stock numbers are related to eastwards distributions and thus low mean ambient temperature. Data from 1978–1984 (Nakken and Raknes, 1987) are however, for some cases, at a distance from this regression line, especially in 1978.

Discussion

For most fish there is a trade-off between optimal food intake and avoiding predation. For cod living in areas with geographical variation in temperature as in the Barents Sea, the ambient temperature would probably also have an influence on this trade-off. In situations where the temperature decreases, the metabolic processes slow down and the maximum food intake will decrease, reducing the growth rates regardless of prey availability (Jobling, 1994). On the other hand, if the

food supply is limited, growth rates may be higher at lower temperatures than in warmer areas due to reduced metabolic costs. For north-east Arctic cod seasonal variation in the consumption of food has been shown. The diet of immature cod is dominated by fish, mainly capelin, and the average contribution of fish preys varies from about 65% in the winter to 35% in the fall (Burgos and Mehl, 1987; Mehl, 1989). In the first half of the year the overlap in the distribution area of immature cod and capelin is maximized (Bogstad and Gjørseter, 1994; Ozhigin *et al.*, 1995). During the winter when the immature cod is feeding, the mature specimens are migrating to the spawning ground along the coast of Norway, while they during autumn are feeding in the northern and eastern part of their distribution area, as described by Jørgensen (1992).

Biases in the estimates

Biases in the estimated lengths at age may originate from several sources and some of them will be discussed later. However, for the data set used here three possible sources of biases are of particular interest;

- (1) The lack of coverage of the easternmost areas prior to 1993 which in some (warm) years may have excluded the smaller fish of the younger age groups from being caught.
- (2) The large codend mesh size (35–40 mm) used prior to 1994 which enabled small sized fish of age 1 (and partly age 2) to escape.
- (3) Our inclusion of length (age) distributions from trawl stations taken for purposes of identification of acoustic scatterers which may have introduced an over-sampling of high abundant concentrations of fish.

With reference to the first type of bias, inspection of the fish distribution maps for the different years (Ottersen *et al.*, 1996) indicated that in 1988, 1989, and 1990, the eastern (and northern) boundaries of cod were well within the area sampled. However, in 1991 and 1992 fish aged 1–3 years were present at several of the easternmost (and northernmost) stations. Catches of older fish ($\text{age} \geq 4$ years) were absent or very low at the boundaries of the surveyed area in all years. It may thus be concluded that insufficient area coverage has generated an upward bias in the annual estimates of length-at-age for ages 1–3 in 1991 and 1992 and also limited the range of input values ($L_{a,int}$, T_{int}) to Equation (5) in these years. Concerning the second type of bias the inability of the trawl to retain small sized specimens prior to 1994 introduced an upward bias in mean length-at-age 1 in all years 1988–1993, and perhaps also of age 2 in some years. However, the 50% retention length of 35–40 mm mesh size is 12–14 cm and unless the actual length distribution of age 2 were highly skewed towards

Table 4. Results of linear regression of mean length at age (L_a) on accumulated mean ambient temperature ($\Sigma\bar{T}_{amb}$) [$L_a = \text{intercept} + \text{slope} * \Sigma\bar{T}_{amb}$]. N represent number of years included in the analysis, L the mean length at age from these years, s.e. is standard error, r^2 is correlation coefficient. Relative increase in length and weight is calculated as percent per °C increase in temperature. Calculated on data from (a) ambient temperature based on swept area densities, 1988–1995 and (b) ambient temperature based on acoustic densities, 1988–1995 (c) ambient temperature based on acoustic densities, 1978–1995.

(a)

Age (years)	N	L (cm)	Intercept (cm) \pm s.e.	Slope (cm °C ⁻¹) \pm s.e.	r ²	(Slope/L)*100 (°C ⁻¹)	3(Slope/L)*100 (°C ⁻¹)
1	8	13	10.6 \pm 1.1	1.29 \pm 0.52	0.51	10	30
2	7	24	12.5 \pm 1.6	2.52 \pm 0.35	0.91	11	33
3	6	37	22.7 \pm 3.1	1.86 \pm 0.39	0.85	5	15
4	5	48	34.7 \pm 3.1	1.21 \pm 0.26	0.87	3	9
5	4	58	44.1 \pm 3.5	0.83 \pm 0.22	0.88	1	3

(b)

Age (years)	N	L (cm)	Intercept (cm) \pm s.e.	Slope (cm °C ⁻¹) \pm s.e.	r ²	(Slope/L)*100 (°C ⁻¹)	3(Slope/L)*100 (°C ⁻¹)
1	8	13	11.6 \pm 0.7	0.77 \pm 0.32	0.49	6	18
2	7	24	16.0 \pm 0.7	1.68 \pm 0.14	0.97	7	21
3	6	37	25.2 \pm 1.5	1.45 \pm 0.18	0.94	4	12
4	5	48	35.2 \pm 1.6	1.07 \pm 0.13	0.96	2	6
5	4	58	42.9 \pm 6.5	0.82 \pm 0.38	0.71	1	3

(c)

Age (years)	N	L (cm)	Intercept (cm) \pm s.e.	Slope (cm °C ⁻¹) \pm s.e.	r ²	(Slope/L)*100 (°C ⁻¹)	3(Slope/L)*100 (°C ⁻¹)
1	18	14	12.3 \pm 0.9	0.83 \pm 0.39	0.23	6	18
2	18	24	18.6 \pm 1.1	1.23 \pm 0.23	0.64	5	15
3	18	35	26.8 \pm 2.1	1.14 \pm 0.27	0.54	3	9
4	17	46	32.9 \pm 3.0	1.18 \pm 0.26	0.57	3	9
5	16	56	39.1 \pm 4.1	1.07 \pm 0.26	0.54	2	6
6	15	65	45.9 \pm 5.7	0.96 \pm 0.29	0.47	2	6
7	14	75	55.5 \pm 9.5	0.82 \pm 0.39	0.27	1	3

smaller lengths it seems unlikely that substantial numbers of that age have escaped the meshes in any year (Table 5). Regarding the third bias, Table 5 shows the deviations between our estimates of mean length-at-age and those obtained from the pre-selected stations used for the computation of swept area indices (Jakobsen *et al.*, 1997; ICES, 1996). Deviations are small and vary in an unsystematic manner in most years. In 1988 and 1993 it appears that our estimates are slightly higher (with the exception of 7-year-olds in 1988 which are much higher) than those corresponding to the swept area indices. The reason for the large difference for 7-year-olds in 1988 is not known.

The effect of the above mentioned biases on the estimated annual growth rates can be qualified as follows:

- Growth rates of age 1 (L_2-L_1) are underestimated in all years prior to 1994 due to upward biased L_1 because small specimens were not retained in the codend.
- The growth rate of age 2 (L_3-L_2) was most likely slightly overestimated in 1990 because of the upward biased L_3 in 1991. In 1991 and 1992 the growth of age 2 was underestimated due to upward biased estimates of L_2 these years.
- Growth rates of age 3 (L_4-L_3) were most likely underestimated in 1991 and 1992 due to upward biased estimates of L_3 those years.

It is unlikely that the estimated relationships between length at age and ambient temperature are seriously affected by these biases for fish of age 2 years and older.

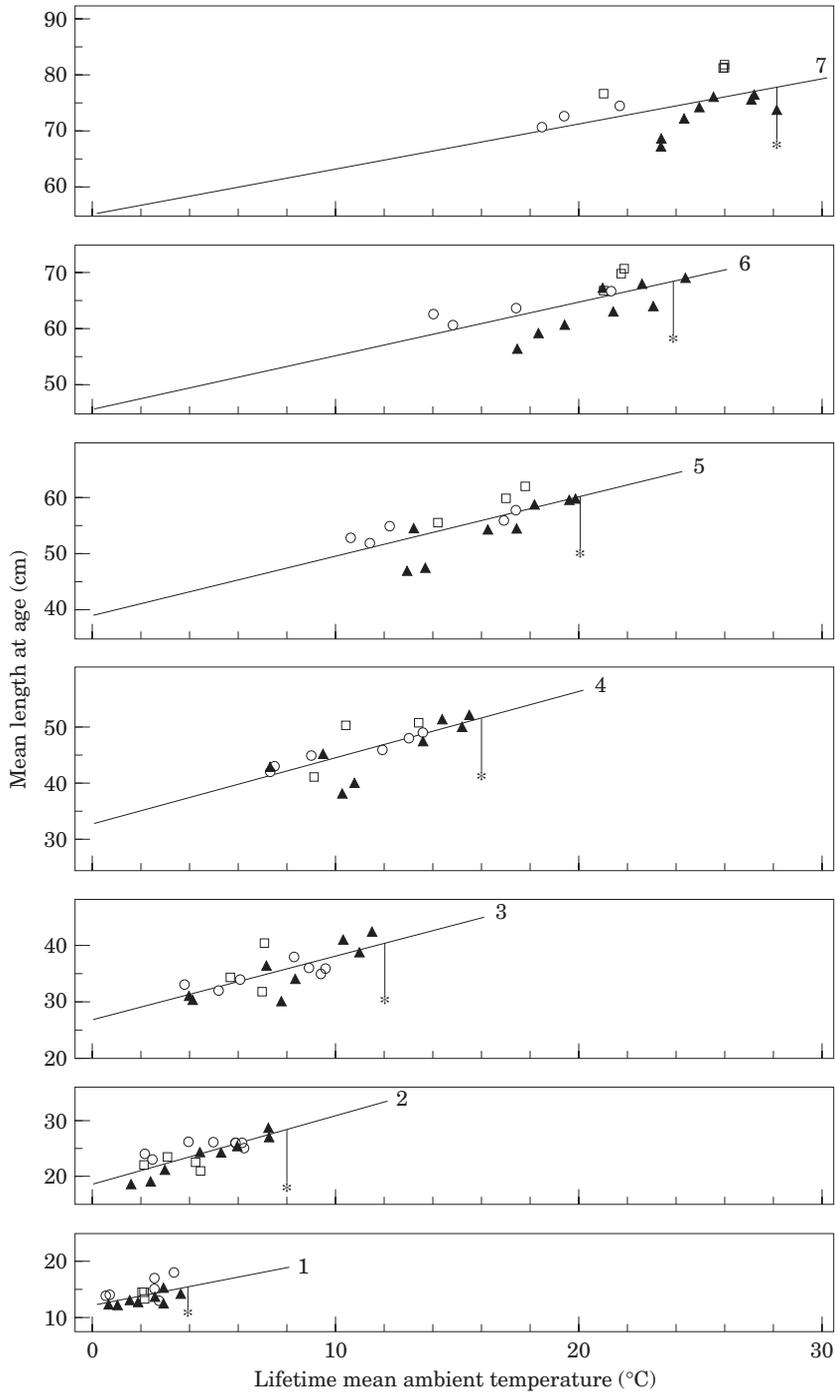


Figure 7. Mean length at age in relation to lifetime mean ambient temperature based on acoustic density estimates and bottom temperature. Triangles indicate data from 1988–1995, squares indicate data from 1985 to 1987, and circles indicate data from 1978 to 1984. Straight lines represent results from linear regressions (Table 4c) when data from all years are used (1978–1995). Numbers to the right indicate age group, while the asterisks represent the mean length at age for cod experiencing a constant temperature of 4°C.

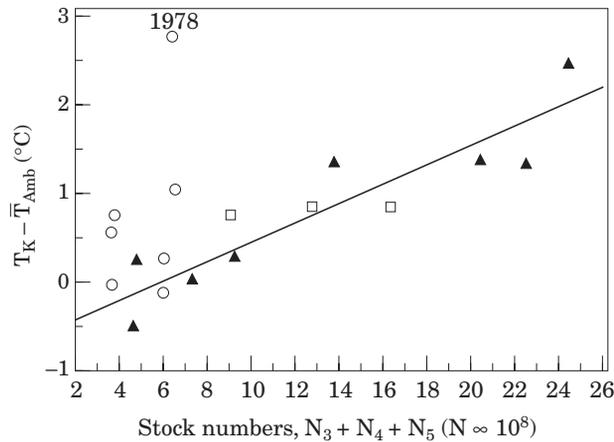


Figure 8. Temperature difference between Kola and mean ambient temperature (acoustic density) for 3-year-old cod related to stock size in numbers * 10⁸ (Anon. 1996). Filled triangles indicate data from 1988 to 1995, squares indicate data from 1985 to 1987 and circles indicate data from 1978 to 1984. The regression line is based on data from 1988 to 1995 (triangles). The year 1978 is outlined.

Table 5. Mean length (cm) at age, L_a, as estimated from all bottom trawl stations and its deviation (mm) from the length-at-age as estimated from preselected stations used for computations of swept area densities (ICES, 1996). Dev. = L_a - L_a (swept area). All values in italics are biased upwards due to the mesh size used and incomplete area coverage.

Age	1988		1989		1990		1991		1992		1993		1994		1995	
	L _a	Dev.	L _a	Dev.	L _a	Dev.	L _a	Dev.	L _a	Dev.	L _a	Dev.	L _a	Dev.	L _a	Dev.
1	<i>15.3</i>	<i>+6</i>	<i>12.5</i>	<i>-2</i>	<i>14.2</i>	<i>-1</i>	<i>13.6</i>	<i>-2</i>	<i>13.2</i>	<i>-2</i>	<i>12.0</i>	<i>+6</i>	<i>12.3</i>	<i>+3</i>	<i>12.5</i>	<i>-2</i>
2	<i>24.3</i>	<i>+18</i>	<i>25.5</i>	<i>-2</i>	<i>28.7</i>	<i>-3</i>	<i>27.2</i>	<i>-4</i>	<i>24.3</i>	<i>-4</i>	<i>21.1</i>	<i>+5</i>	<i>18.5</i>	<i>0</i>	<i>19.1</i>	<i>+3</i>
3	<i>30.3</i>	<i>+6</i>	<i>34.4</i>	<i>-3</i>	<i>38.8</i>	<i>-6</i>	<i>42.5</i>	<i>+9</i>	<i>41.1</i>	<i>-2</i>	<i>36.4</i>	<i>+5</i>	<i>31.0</i>	<i>+5</i>	<i>30.4</i>	<i>+5</i>
4	<i>38.2</i>	<i>+12</i>	<i>40.3</i>	<i>-3</i>	<i>47.6</i>	<i>+2</i>	<i>52.3</i>	<i>+3</i>	<i>50.2</i>	<i>-5</i>	<i>51.4</i>	<i>+5</i>	<i>45.2</i>	<i>+4</i>	<i>43.0</i>	<i>+5</i>
5	<i>47.3</i>	<i>+9</i>	<i>47.8</i>	<i>+3</i>	<i>54.6</i>	<i>+7</i>	<i>59.1</i>	<i>-11</i>	<i>60.1</i>	<i>+2</i>	<i>59.7</i>	<i>+5</i>	<i>54.8</i>	<i>-2</i>	<i>54.6</i>	<i>+4</i>
6	<i>59.6</i>	<i>+16</i>	<i>56.7</i>	<i>-4</i>	<i>61.1</i>	<i>+2</i>	<i>67.6</i>	<i>+6</i>	<i>68.7</i>	<i>-5</i>	<i>69.6</i>	<i>+8</i>	<i>64.5</i>	<i>-1</i>	<i>63.7</i>	<i>-2</i>
7	<i>74.6</i>	<i>+45</i>	<i>67.7</i>	<i>-8</i>	<i>69.1</i>	<i>-18</i>	<i>72.7</i>	<i>-11</i>	<i>76.7</i>	<i>-3</i>	<i>77.0</i>	<i>+8</i>	<i>74.4</i>	<i>+9</i>	<i>76.2</i>	<i>+2</i>

Both ambient temperatures and mean lengths were calculated using the same fish densities as weights in the calculations. Since the smaller specimens inhabit colder waters an upward bias in mean length due to uncovered cold areas are accompanied by an upward bias in ambient temperature. Hence the slopes in Equations (5) and (11) will be effected to a much lesser extent than the annual growth rates. The main drawback introduced by uncovered areas in 1991 and 1992 is the limitation of range in the data of both lengths and temperature, which reduces the precision in the estimated slopes.

In addition other sources of errors may have biased the results. Large fish, in warm areas, could be capable of maintaining swimming speeds of more than 3 knots for longer time periods than 30 min, which is the duration and speed of the trawl hauls. In the cold areas, small fish, less than 20 cm in length, will probably have a lower swimming speed than the herding speed of the sweeps (He, 1991, 1993). If such a temperature dependent capture efficiency has affected our data, this implies

that we have underestimated the effect of temperature and the regression line could have been steeper for the youngest (1 and 2) and oldest (6 and 7) age groups. The reduction in slopes with age can also be an effect of commercial fishing, which will remove the fastest growing specimens at an increasing rate from age 3 to age 5-6 when cod recruits to the fishery. In addition, mature 6 and 7-year-old cod will be outside the survey area on their spawning migration during the time of the survey. Michalsen *et al.* (1996) have observed diurnal variation in catchability of cod at a fixed trawl location. They found that tidal currents can affect the vertical distribution of cod and haddock and thus the availability to the bottom trawl. In addition light intensity can affect the catch efficiency of the sampling trawl, resulting in diurnal variation in catch rates and length frequency distribution. This was also observed by Engås and Soldal (1992). On the other hand, Ren (1993) reported that no clear diurnal pattern in acoustic densities was observed in the vertical distribution of cod and haddock

when data collected over a month and with continuously diurnal sampling was combined. However, further investigations and quantification on the effect of vertical distribution on the abundance indices ought to be carried out.

Geographical and temperature related distribution of length-at-age

Along with the reduction in temperature with longitude there are observed geographical variations in mean length of cod within each age group from east to west. Since the distribution area of the various age groups will change from year-to-year with abundance as well as with temperature (Ottersen *et al.*, 1998), differences in mean length between fixed geographical areas as presented in Table 2, may not represent the full range of differences in length-at-age in the stock. The tendency that the age groups maintain their horizontal distribution relative to each other, more or less independent of the absolute values of temperature (Ottersen *et al.*, 1998) introduces an interannual variation in any comparisons of length-at-age around a certain longitude or latitude.

In most years the length-at-age with increasing temperature for the age group 2–6, was larger in warmer waters than in colder (shown also by Loeng, 1989). The amplitude or range of the cod's seasonal migrations increases with fish size/age (Mehl *et al.*, 1985; Nakken, 1994) and hence the larger fish in an age group conduct more extensive south- and westward directed winter migrations than do the smaller individuals. Thus, the positive relationship between length-at-age and temperature experienced in most of the years is probably a result of this size dependent seasonal migration and should not be interpreted as temperature dependent growth. The geographical and temporal distribution of immature cod in winter is to a large extent determined by the south-westward movement of pre-spawning capelin, the cod's main prey item. Year-to-year therefore, shifts of the capelin migration may be the main cause of the large interannual variations in the estimated relations between length-at-age and temperature. For some age groups the tendency of larger fish to be in warmer waters appeared to be absent in one or two of the years studied here.

Growth and mean ambient temperature

The positive relationship between mean length-at-age in cod and temperature can reflect a length dependent horizontal distribution associated with size dependent seasonal migrations rather than a temperature dependent growth, as discussed earlier. However the annual growth rates (absolute and instantaneous) also appeared to be positively related to annual mean ambient temperatures.

The 1 year delay of the maximum in the weight increments as compared with the length increments in Figure 4 is a consequence of the weight-length relationship; the bigger the fish the larger are the annual weight increments, particularly in periods of good growth. Relatively high growth rate of 2-year-old cod in 1991 is a result of insufficient coverage of the eastern part of the distribution area of young cod (Aglen and Nakken, 1997). The decrease in instantaneous growth rate, both in length and weight, coincided with decreasing mean ambient temperatures (Fig. 5). The apparent time lag between growth maximum and temperature is an effect of the poor resolution in the temperature data. The most intense warming of the Barents Sea in recent years occurred during spring and summer 1989 (Loeng *et al.*, 1992). The temperature in the Kola section increased by almost 3°C from February to September. Hence the actual ambient temperatures in 1989 were probably considerably higher than our data from February in Figure 5 indicate. Ottersen *et al.* (1998) found that the young North-east Arctic cod responded to an increase in population size in 1990–1993 with an easterly range extension, resulting in lower ambient temperatures. Our results show that the increase in abundance over those years also was accompanied by reduced growth (Figs 4 and 5). Theoretically, assuming a growth-density relationship, the individual predators high abundances will have reduced food rations and thus experience a reduction in the growth rates (Nilssen *et al.*, 1994). Stomach analysis shows that cod larger than 20 cm (about 2 years of age) incorporate fish in the diet, and that the most important prey species is capelin (Mehl, 1989, 1991). In the period from 1990 to 1993 the abundance of capelin increased greatly (Gjøsæter, 1997) and led to an increase in individual consumption of capelin by cod (Bogstad and Mehl, 1997). Consequently the observed reduction in growth rate in this period was not due to a reduction in prey availability. When cod are more abundant a higher proportion of the stock may inhabit areas with lower temperatures than they normally would and hence the growth rates will decrease in those years compared to years of lower abundance. Hence a growth-temperature relation may wrongly be interpreted as a growth-density (abundance) relation when only biological data are being used in the analyses.

Mean individual growth, in terms of mean length-at-age, between age 1 and age 4 was significantly higher for year classes experiencing higher temperatures than for year classes inhabiting colder waters. Both Figure 6 and Table 4 reveal considerable differences in slopes depending on whether swept area based or acoustic based ambient temperatures are used in the analyses. Mean ambient temperature, based on swept area estimates yields slopes between 0.8 and 2.5 cm °C⁻¹, decreasing with age (Table 4a). In comparison the slopes when

using mean ambient temperature based on acoustic densities (Table 4b) are substantially less for all age groups due to a wider temperature range. As stated by Ottersen *et al.* (1998) we cannot evaluate which of the two sets of ambient temperatures are more representative. This will probably vary from year-to-year with the vertical distribution of the fish and thus their availability to the sampling methods (swept area or acoustics) will also display. It will also be affected by the temperature-dependent capture efficiency which will bias the swept area densities and mean length-at-age as commented on previously. When data from as far back as 1978 were included in the analysis the dependence of growth on temperature decreased considerably for 2 and 3-year-old fish as compared with the results from 1988 to 1995. These data include one of the coldest periods ever observed in the Barents Sea (1978–1981) (Tereschencko, 1996). As seen from Figure 5 the temperature range is increased and the slope values reduced. In addition the approach taken to fill in the missing data for 1985–1987 is in conflict with the argument that cod distribution changes with abundance, reducing the reliability of the calculated mean ambient temperatures for those years.

In recent years several growth studies on cod have been carried out, mostly based on small-scale laboratory experiments with restricted number of fish, size- and temperature range. Jobling (1988) has combined some of these results and gives an equation for the effect of temperature and fish size on the growth of cod. In the temperature range experienced by North-east Arctic cod (1–6°C), Jobling's equation gives an increase in growth rate (weight) of 25–30% per °C increase in temperature for all sizes of fish, corresponding to 8–10% increase per °C in length. In our results (Table 4 and Fig. 7) the effect of temperature on the mean length-at-age appears to be absent for cod older than 2 years. Slopes increased from age 1 to age 2 in all the three data series used, indicating a gain in growth with increasing temperature up to age 2. However, for older ages slope values were approximately equal or decreasing with age, indicating no gain or even a reduced growth with increasing temperature. This, as discussed previously is probably due to the fishery which removes the faster growing specimens at an increasing rate when cod reach an age of 3–5 years. From analysis of 17 North Atlantic cod stocks Brander (1994, 1995) found an almost 30% increase in weight at age 4 for each degree increase in temperature. Brander's finding corresponds to an approximate increase in length of 10% per degree in temperature, a result which is three times those appearing from Table 4c and twice as high as those in Table 4a and 4b.

At age 3 cod start to extend their seasonal migrations farther south and west during the wintertime (Ottersen *et al.*, 1998) and farther to the north and east where they feed during the summer and autumn (Woodhead and

Woodhead, 1965; Mehl *et al.*, 1985) and the extent of these migrations will increase with age. Due to these seasonal migration patterns, the ambient winter temperature used here is probably close to the annual maximum values (Godø and Michalsen, 1997). According to Figure 5 the mean ambient winter temperature for the period 1988–1995 has a range of 2.5–4.0°C depending on age. The range in the annual minimum of ambient temperature is most likely to be substantially less. The annual minimum occurs in late summer/autumn when the fish are feeding along the Polar front; the transition zone between Arctic and Atlantic water masses, which has the same temperature each year. Consequently, the actual annual means of ambient temperature as well as the differences between these means are lower than the values used here. The present analyses therefore, probably underestimated the effect of temperature on growth.

For pelagically distributed 0-group cod (0–60 m depth) Loeng *et al.* (1995) observed faster growth during the summer and a greater mean length of the year classes in August in warm years than in cold, while Helle (1994) however, found no relationship between mean lengths and temperature within a particular year. Our finding that the mean length-of-age 1 is not related to temperature is not necessarily in contradiction with the observation of Loeng *et al.* (1995). 0-group cod descend from the upper layers in autumn and then their environment is greatly changed. Ambient temperature is substantially reduced and the mortality remains high and variable (Ottersen *et al.*, 1998); both of these were factors that may change the mean length-temperature relationship of the year class prior to our observations in February. Also the estimated mean lengths of age 1 cod are uncertain due to length selective sampling.

Growth of North-east Arctic cod has been estimated by a bioenergetic model (Aijad, 1996), where temperature is an important variable. The temperatures used in that model are monthly climatological temperatures (Ottersen and Ådlandsvik, 1993) in three fixed locations which are regarded as representative for the western, eastern, and northern parts of the Barents Sea with some interannual correction due to monthly mean temperatures in the Kola section. As shown by Ottersen *et al.* (1998) these are significantly higher for the period 1991–1995 than our estimates of ambient temperature, leading to an overestimation of the consumption estimates by as much as 10–30%.

Mean ambient temperature and abundance

The relationship between stock abundance and difference between mean ambient temperature and the temperature in the Kola section, is quite good for the years 1988–1995. When looking at the older data the year 1978 is an outlier. Nakken and Raknes (1987) suggested

that incomplete coverage of the western (warm) areas resulted in an underestimation of the mean ambient temperature in 1978. In addition, a pronounced cooling of the Barents Sea took place during that year, starting in the eastern areas, followed by an extensive westward displacement of all age groups of cod (Midttun *et al.*, 1981). Hence the temperature difference between Kola and the mean ambient temperature probably is heavily overestimated for 1978. At high stock abundances the distribution of North-east Arctic cod covers larger areas, increasing the abundance relatively more in marginal habitats (Ottersen *et al.*, 1998) resulting in reduced growth. This is also in accordance with findings on Norwegian spring-spawning herring where reduced growth at high stock abundance is assumed to be a result of extended geographical distribution into areas with lower temperature (Toresen, 1990).

In this study differences in length and weight between two age groups of the same year class have been used to calculate mean individual growth. In order to get more exact measurements of the effect of temperature on growth of cod the temperature that the fish are experiencing during summer–autumn should be calculated. In addition use of data storage tags, which measure depth and temperature in the surroundings of the individual fish (Godø and Michalsen, 1997), can provide more detailed information in the future.

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References

- Aglen, A., and Nakken, O. 1997. Improving time series of abundance indices applying new knowledge. *Fisheries Research*, 30: 17–27.
- Ajjad, A. M. 1996. Assessing growth of Northeast Arctic cod by a bioenergetics model. *ICES CM 1996/G*: 16, 14 pp.
- Bogstad, B., and Gjøseter, H. 1994. A method for estimating the consumption of capelin by cod in the Barents Sea. *ICES Journal of Marine Science*, 51: 273–280.
- Bogstad, B., and Mehl, S. 1997. Interactions between cod and its prey species in the Barents Sea. Proceedings of the International Symposium on the role of forage fish in Marine Ecosystems, Anchorage, Alaska, November 13–16, 1996. 23 pp.
- Brander, K. 1994. Patterns of distribution, spawning and growth in North Atlantic cod—the utility of inter-regional comparisons. *ICES Marine Science Symposia*, 198: 406–413.
- Brander, K. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). *ICES Journal of Marine Science*, 52: 1–10.
- Brett, J. R. 1979. Environmental factors and growth. *In* Fish physiology, vol. VIII, pp. 599–675. Ed. by W. S. Hoar, D. J. Randall, and J. R. Brett. Academic Press, New York.
- Burgos, G., and Mehl, S. 1987. Diet overlap between North-East Arctic cod and haddock in the southern part of the Barents Sea in 1984–1986. *ICES CM/G*: 50.
- Clarke, A. 1993. Seasonal acclimatization and latitudinal compensation in metabolism: do they exist? *Functional Ecology* 7: 139–149.
- Daan, N. 1994. Trends in North Atlantic cod stocks: a critical summary. *ICES Marine Science Symposia*, 198: 269–270.
- Engås, A., and Soldal, A. V. 1992. Diurnal variations in bottom trawl catches of cod and haddock and their influence on the abundance indices. *ICES Journal of Marine Science*, 49: 89–95.
- Godø, O. R., and Michalsen, K. 1997. The use of Data Storage Tags to study cod natural behaviour and availability to abundance surveys in the Barents Sea. *ICES CM 1997/W*: 18. 23 pp.
- Gjøseter, H. 1997. The Barents Sea capelin stock—A brief review. Proceedings of the International Symposium on the role of forage Fish in Marine Ecosystems, Anchorage, Alaska, November 13–16, 1996.
- He, P. 1991. Swimming endurance of Atlantic cod, *Gadus morhua* L., at low temperatures. *Fisheries Research*, 12: 65–73.
- He, P. 1993. Swimming speeds of marine fish in relation to fishing gears. *ICES Marine Science Symposia*, 196: 183–189.
- Helle, K. 1994. Distribution of early juvenile Arcto-Norwegian cod (*Gadus morhua* L.) in relation to food abundance and watermass properties. *ICES Marine Science Symposia*, 198: 440–448.
- ICES. 1996. Report of the Arctic Fisheries Working Group. *ICES CM 1996/Assess*: 4, 311 pp.
- Jakobsen, T., Koresbrekke, K., Mehl, S., and Nakken, O. 1997. Norwegian combined acoustic and bottom trawl surveys for demersal fish in the Barents Sea during winter. *ICES CM 1997/Y*: 17. 26 pp.
- Jakobsson, J. 1992. Recent variability in the fisheries of the North Atlantic. *ICES marine Science Symposia*, 195: 291–315.
- Jobling, M. 1988. A review of the physiological and nutritional energetics of cod, *Gadus morhua* L., with particular reference to growth under farmed conditions. *Aquaculture*, 70: 1–19.
- Jobling, M. 1994. Fish bioenergetics. Chapman and Hall, London. 309 pp.
- Jørgensen, T. 1992. Long-term changes in growth of North-east Arctic cod (*Gadus morhua*) and some environmental influences. *ICES Journal of Marine Science*, 49: 263–277.
- Loeng, H. 1989. The influence of temperature on some fish population parameters in the Barents Sea. *Journal of Northwest Atlantic Fisheries Science*, 9: 103–113.
- Loeng, H., Blindheim, J., Ådlandsvik, B., and Ottersen, G. 1992. Climatic variability in the Norwegian and Barents Sea. *ICES Marine Science Symposia*, 195: 52–61.
- Loeng, H., Bjørke, H., and Ottersen, G. 1995. Larval fish growth in the Barents Sea. *Canadian special Publication of Fisheries and Aquatic Sciences*, 121: 691–698.
- Mehl, S. 1989. The Northeast Arctic cod stock's consumption of commercially exploited prey species in 1984–1986. *Rapports et Proces-Verbaux des Reunions du Conseil International pour l'Exploration de la Mer*, 188: 185–205.
- Mehl, S. 1991. The Northeast Arctic cod stock's place in the Barents Sea ecosystem in the 1980s: an overview. Ed. by E. Sakshaug, C. C. E. Hopkins and N. A. Øritsland. *In* Proceedings of the Pro Mare Symposium on Polar Marine Ecology, Trondheim, 12–12 May 1990. *Polar Research*, 10: 525–534.

- Mehl, S., Nakken, O., Tjelmeland, S., and Ulltang, Ø. 1985. The construction of a multispecies model for the Barents Sea with special reference to the cod-capelin interactions. *Contr. Workshop comparative biology, assessment and management of gadoids from the North Pacific and Atlantic oceans*. Seattle, 24–28 June 1985, pp. 1–25.
- Michalsen, K., Godø, O. R., and Fernö, A. 1996. Diel variation in the catchability of gadoids and its influence on the reliability of abundance indices. *ICES Journal of Marine Science*, 53: 389–395.
- Midttun, L., Nakken, O., and Raknes, A. 1981. Variations in the geographical distribution of cod in the Barents Sea in the period 1977–1981. *Fisken Havet* No. 4, 1981: 1–16. (In Norwegian).
- Nakken, O. 1994. Causes of trends and fluctuations in the Arcto-Norwegian cod stock. *ICES Marine Science Symposia*, 198: 212–228.
- Nakken, O., and Raknes, A. 1987. The distribution and growth of Northeast Arctic cod in relation to bottom temperatures in the Barents Sea, 1978–1984. *Fisheries Research*, 5: 243–252.
- Nilssen, E. M., Pedersen, T., Hopkins, C. C. E., Thyholt, K., and Pope, J. G. 1994. Recruitment variability and growth of Northeast Arctic cod: influence of physical environment, demography, and predator-prey energetics. *ICES Marine Science Symposia*, 198: 449–470.
- Ottersen, G., Michalsen, K., and Nakken, O. 1996. Ambient temperature and distribution of Northeast arctic cod. *ICES CM 1996/G*: 13. 40 pp.
- Ottersen, G., Michalsen, K., and Nakken, O. 1998. Ambient temperature and distribution of North-east Arctic cod. *ICES Journal of Marine Science*, 55: 67–85.
- Ottersen, G., and Ådlandsvik, B. 1993. Climatological temperature and salinity fields for the Nordic Seas. Institute of Marine Research Department of Marine Environment. Report no. 8, 1993. 121 pp.
- Ozhigin, V. K., Tretyak, V. L., Yaragina, N. A., and Ivshin, V. A. 1995. Growth of Arcto-Norwegian cod in dependence of environmental conditions and feeding. *ICES CM*, 1995/P: 10, 16 pp.
- Ponomarenko, V. P. 1967. Reasons for changes in the rate of growth and maturation in the Barents Sea cod. *ICES CM*. 1975/F: 10, 8 pp.
- Ren, S. 1993. Changes in catchability of Barents Sea cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) related to varying availability to the bottom trawl survey. Master of Philosophy thesis. University of Bergen, Norway. 49 pp.
- Shevelev, M. S., Tereschchenko, V. V., and Yaragina, N. A. 1987. Distribution and behaviour of demersal fishes in the Barents and Norwegian Seas, and the factors influencing them. *In* The effect of oceanographic conditions and distribution and population dynamics of commercial fish stocks in the Barents Sea. Proceedings of the third Soviet-Norwegian Symposium, Murmansk, 26–28 May 1986. Ed. by H. Loeng. Institute of Marine Research, Bergen. 250 pp.
- Tereschenko, V. V. 1996. Seasonal and year-to-year variations of temperature and salinity along the Kola meridian transect. *ICES CM*. 1996/C: 11, 24 pp.
- Toresen, R. 1990. Long-term changes in growth of Norwegian spring-spawning herring. *Journal du Conseil International pour l'Exploration de la Mer*, 47: 48–56.
- Woodhead, P. M. J., and Woodhead, A. D. 1965. Seasonal changes in the physiology of the Barents Sea Cod *Gadus Morhua* L., in relation to its environment. II. Physiological reactions to low temperatures. *ICNAF Special Publication*, 6: 717–734.
- Wootton, R. J. 1990. Ecology of teleost fishes, pp. 117–158. Chapman and Hall, London. 404 pp.