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GROWTH OF NORTHEAST ARCTIC COD IN RELATION TO AMBIENT TEMPERATURE.

by

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ABSTRACT

In the present study temperature related changes in horizontal distribution are described and the influence of temperature on the growth of Northeast Arctic cod is interpreted. Data from acoustic-and bottom trawl surveys in the Barents Sea each February 1988-1995 has been used to relate mean length at age to the ambient winter temperature. Mean lengths at age increased with increasing temperature for ages greater than 2 years. Individual mean growth between age 1 and age 4 was significantly higher for yearclasses (cohorts) experiencing higher temperatures than for yearclasses inhabiting colder waters. Our use of estimates of ambient temperature in February instead of annual mean values probably introduces an underestimation of the temperature effect on growth. Increased abundance of young cod is associated with an extension of the distribution area towards east and north into colder water. Hence a growth temperature relation may wrongly be interpreted as a growth-density (abundance) dependency if ambient temperature is not included in the analysis.

INTRODUCTION

Fishes are characterized by having extremely plastic and highly variable growth (Weatherly, 1972). Moreover, some of the ecological parameters known to influence growth as food availability, stock abundance, temperature and others, are either difficult to estimate in the field or their effects on the fish population are mediated through a complex structure of processes operating in the ecosystem, and are therefore not straightforward to quantify (Jonsson, 1965; Houghton and Flatman,1981; Jobling, 1982; Mehl and Sunnanå, 1990; Steinarsson and Stefansson, 1991; Jørgensen, 1992; Suthers and Sundby, 1993; Daan and Heesen, 1994; Jakupsstovu and Reinert, 1994). Although many features of the environment differ between summer and winter a great deal of attention has been directed at understanding the effects of changes in temperature. This is partly because environmental temperature after all is one of the simplest parameters to measure and record (see Vogel, 1981), but also because the temperature in some way or another effects almost all specimens in the ecosystem, and thereby makes it an important indicator for changes in i.e fish population dynamics (Jobling, 1995).

Brander (1995) who examined 17 North Atlantic cod stocks including Northeast Arctic cod found that most of the observed variability in growth was due to changes 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".

For the Northeast Arctic cod year-to year changes in growth have been observed over a long time period (Nakken, 1994; Ozhigin, V. K. et al., 1995). An inverse relation between growth and stock abundance has been taken as an evidence of density-dependent growth (Ponomarenko, 1967; Jørgensen, 1990; Nilssen et al., 1994), while Nakken and Raknes (1987) explained an increase in length at age as an effect of increasing temperatures, although the total stock size declined rapidly during the same period.

Our understanding of the factors controlling growth rate and especially how these factors interact is still incomplete. In the present study temperature related changes in horizontal distribution are described and the influence of temperature on the growth of Northeast Arctic cod is interpreted. It is mainly growth in terms of changes in length that is investigated, but also changes in weight at age, abundance (biomass) and consumption/biomass ratios are discussed. Data from acoustic-and bottom trawl surveys in the Barents Sea each February 1988-1995 has been used to relate mean length at age to the ambient winter temperature.

MATERIAL AND METHODS

The material.

The data used in this study originate from combined bottom trawl and acoustic surveys in the Barents Sea, conducted in February each year from 1988-1995. Until 1992 the area covered by the bottom trawling was limited to a certain standard area (Ottersen *et al.,* 1996). Since 1993 the two areas have been expanded to the north and east in order to cover the geographical distribution of the younger age groups of cod satisfactorily. During the cruises also CTD profiles are taken throughout the whole Barents Sea. The number of stations have been between 148 (1989) and 389 (1995). The CTD temperatures were, from the database's vertical resolution of 5 meters, interpolated vertically to a single horizontal field in two manners. To represent the bottom temperature the average of the two lowermost depth levels from each station were used, while the average from 100 m depth to bottom was taken to represent the temperature of the total vertical range inhabited by the cod (see Ottersen *et al.*, 1996).

In the bottom trawl surveys a shrimp trawl (Campelen 1800) has been used. Further specifications on equipment and methods are given in Korsbrekke *et al.* (1995) and Aglen and Nakken (1996). Density estimates (number of fish per square nautical mile, ρ) were calculated for each 5 cm length group.

$$\rho = c / (d\ s) \qquad \text{(I)}$$

where c is numbers at length in the catch

d is distance towed; i.e. length of swept area

s is effective spread; i.e. width of swept area

Equation I was applied haul by haul and we have computed densities from bottom trawl stations in predetermined positions as well as from catches taken for identification of acoustic scatters. At selected trawl stations otoliths from two fish at each 5 cm interval were collected and the age read, giving an age/length key for each of five different sub areas (Korsbrekke *et al.*, 1995). Densities at length at each station were converted to densities at age by applying the appropriate age/length keys. An average density at age was computed for each temperature interval and multiplied by the area of the interval in order to arrive at numbers at age at temperature intervals. For each age group stations with less than 100 fish per square nautical mile were excluded in the further calculations. The number of trawl stations for each age group is given in Table 1. Figure 1 shows the distribution of density estimates at stations for the 3 and 5 year old cod in 1990 and 1994 within each temperature interval.

Estimates.

The mean length at age, $\overline{L}$, is defined by the equation:

$$\overline{L} = \sum \rho_i \cdot L_i / \sum \rho_i \qquad \text{(II)}$$

where i denotes length group and ρ is the density at age (numbers per unit area). Mean length were calculated for each station each year, $\overline{L}_s$, for temperature interval, $\overline{L}_{int}$, and for year, $\overline{L}$, by including the appropriate data sets in the summarising in equation II.

Mean weights at age as well as numbers at age were taken from Korsbrekke *et al.* (1995) and used to calculate biomass. A series of consumption/biomass ratios which presumably indicate the variation by age was taken from the report of the Arctic Fisheries Working Group (Anon. 1996).

Estimates of the temperature of the water masses actually surrounding the fish, the ambient temperature, have been taken from Ottersen *et al.* (1996), where it was defined as density weighted temperature means for each agegroup. Four estimates of ambient winter temperature for each age and year were computed by combining each of the two types of density estimates (acoustic and swept area) with the temperature at the bottom and the average temperature in the 100m depth to bottom layer (Ottersen *et al.,* 1996). Maps of bottom temperature and mean lengths at age at trawl stations have been examined for all years of investigation, but due to limited space only a few are presented in the paper.

Analyses.

Mean length at age and geographical distribution.

Differences in mean length at age in western and eastern areas were for each year analysed by using the following expression:

$$\Delta L = \overline{L}\ (\text{West of } 20\ °E) - \overline{L}\ (\text{East of } 35\ °E) \qquad \text{(III)}$$

where the mean values were obtained by applying equation II for each of the two areas.

Distribution of mean length at age on temperature.

In an attempt to quantify the relationship between length at age and temperature the estimated mean length at age in each temperature interval ($\overline{L}_{int}$) was related to temperature (T) through a linear regression:

$$L = \text{Intercept} + \text{Slope} * T \qquad \text{(IV)}$$

The regression was made for each year separately as well as for all years combined.

We are mainly interested in the slope values in the above equation and 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. This is easily seen if two years having equal slopes but with different intercepts are considered. If in one of these years data is available for only a part of the total combined range then 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.

In order to avoid such a bias and to investigate the magnitude of the possible bias introduced by the procedure used above, we therefore computed an overall slope as the weighted mean of each years slope using the inverse of the standard error as weight;

$$\text{Weighted slope} = \left(\sum_{i=1988}^{1995} slope_i \cdot \frac{1}{SE_i} \right)_i \Big/ \left(\sum_{i=1988}^{1995} \frac{1}{SE_i} \right) \qquad \text{(V)}$$

Growth and ambient temperature.

The absolute growth rate was defined as the length or weight increment during one calendar year:

g_i (length) = $(L_{i+1}-L_i)$ and (VI)

g_i (weight) = $(W_{i+1}-W_i)$ (VII)

The specific annual growth rate was calculated as:

$$g_i(\text{length}) = (\ln L_{i+1} - \ln L_i) \qquad \text{(VII)}$$

$$g_i\,(\text{weight}) = (\ln W_{i+1} - \ln W_i) \qquad \text{(VIII)}$$

where L_i (W_i) and L_{i+1} (W_{i+1}) are the length (weight) of the same year class when of age i and i+1 respectively.

In an attempt to establish a relation between mean length at age and mean ambient temperature, data from Nakken and Raknes(1987) were included in the analysis. However, there are three years between theirs and our data that are not covered. For these years (1985-1987) length at age were taken from Korsbrekke *et al.*, (1995), while estimates of ambient temperature were calculated by linear regression analyses between existing ambient temperatures (T_i, 1978-1995) and monthly 0-200 m depth sea temperature averages from the Kola-section (Bochkov, 1982).

The relation between length at age and temperature was further investigated by summing up the ambient temperatures that each age group had experienced during their life, the accumulated ambient temperature, and performing linear regressions analyses between these values and mean lengths at age ($\overline{L_i}$), combined for all year classes.

$$\overline{L} = \text{Intercept} + \text{Slope} * T \qquad \text{(IX)}$$

where T is mean accumulated ambient temperature for each age group and year class.

RESULTS AND DISCUSSION

Horizontal 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 years old cod for the years 1990 and 1994 (Figure 2). For both these age groups and years the isolines 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 °C isotherm from west to east, with considerable smaller fish in the areas east of that isotherm than farther west. In 1990 mean lengths of age group 3 were generally higher than in 1994, but for 5 year old fish the difference between the two years were less. Differences in length at age between the western (warm) and eastern (cold) part of the area are summarized in Table 2. Positive values, indicating bigger fish in the western area, were found in most years for age groups 3-5 with the greatest differences in 1990 and 1991 for 3 year old fish. It should be noted that the values in Table 2 are mean values for fixed geographical areas. 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.*, 1996), such mean values may not represent the actual differences in length between the western and eastern parts of each age groups distribution.

In Table 3 mean lengths at age by temperature and year are shown. Most years the main tendency is that lengths increase with increasing temperature, particularly for age groups 2-5 years although mean lengths at age for a given temperature interval vary considerably between years. This may indicate that the length-temperature related horizontal distribution pattern of these agegroups are affected by the mean length of the age group (i.e. the growth in proceeding years) only to a minor extent. Size- and temperature dependent capture efficiency may also have biased the estimates in Table 3 (Ottersen *et al.*, 1996). In the high temperature range the estimated lengths of large (old) fish might be too low while the low temperature range the estimates of mean lengths of the 1-group probably are too high. In addition a considerably amount of mesh selection of 1-and partly 2-group cod took place prior to 1994, so that for the years 1988-1993 the estimated mean lengths of the 1-group and to some extent also those of the 2 year olds definitely are biased upwards. Michalsen et al. (1996) have observed diel variation in mean length of cod but how strongly this affect data collected over a month og continuously sampling is still not quantified.

The relationship between length at age and temperature.

Figure 4 and Table 4 shows the results of linear regressions of length at age on mean ambient temperature. Although a considerable scatter appears, nearly all slope values are positive for 3-5 year old fish indicating a positive relation between length at age and temperature: The higher the temperature than larger are the fish. For age 1 there is no such pattern and for the 2, 6 and 7 year olds several years with negative or near zero slope values were found. Thus, an eventual relation between length and temperature for these age groups is much weaker than for the 3-5 years olds. The tendency towards bigger fish in warmer waters becomes quite pronounced in the two curves (Figure 4, Table 4 and Figure 5) which represents the "mean" for the 8 years of observations. The slopes of the full drawn curves representing the results from linear regressions using data for all years combined, may however be overestimates as explained previously. The method of making 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 indicate an average length dependency of 1-2 cm per degree centigrade indicating that fish in the south western warm areas with temperatures of 5-6 ^{0}C (Figure 2) commonly are 5-10 cm greater in length than those in the eastern low temperature areas (0-1^{0}C) (Loeng, 1989). This corresponds to a relative length difference of 15-29 percent at a mean length of 35 cm (Table 3). Since the relative change in weight is about 3 times the relative change in length it indicates that 3 year olds in the south western area weight almost twice as much as specimens of that age in the eastern parts of the distribution area.

Growth and mean ambient temperature.

Figure 6 shows the annual length-and weight increments of each age group during the period of observation (note that the increments from age i to age i+1 are taken from February to February and plotted in the middle of the calendar year the fish was aged i). Growth increased from an historic low value experienced in 1986-1988 (Anon., 1996) to a maximum in 1989-1990 for all age groups. The one year delay of the maximum in weight increments as compared with length increments is just a consequence of the weight-length relation; the bigger the fish the larger are the annual weight increment, particularly in periods of good growth. From 1990 and onwards growth decreased for all age groups reaching a minimum in 1993.

Specific annual growth rates in length and weight are presented in Figure 7 where also the development of ambient temperature, biomass and consumption/biomass ratio are given for comparison. The general patterns in specific growth rates are similar to those seen in Figure 6 except that the delay between growth in weight and length now is removed. It may look as if there is a time lag between growth maxima and the maximum in ambient temperature but this may be artificial, due to the poor resolution (one year) in temperature data. The most intense warming of the Barents Sea in recent years occurred during spring and summer 1989 (Loeng *et al.*, 1992). Then 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 indicate.

When comparing the graphs in Figure 7 the main impression is that the reduction in growth 1990-1994 coincided with a decrease in ambient temperature. It also coincided with an increase in abundance (biomass) and with a decrease in the consumption/biomass ratio. As shown by Ottersen *et al.* (1996) the increase in abundance during the early 1990's was accompanied by an extension of the distribution area of young cod. East-and northward extensions of the distribution area inevitably lead to lower ambient temperatures. Consequently it appears that an increased abundance of young cod will effect the ambient temperature as well as the availability of food (lower graph Figure 7) in a manner that may effect growth rates negatively. 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.

In Figure 8 mean lengths at age of each year class are plotted against accumulated ambient temperatures (accumulated over the lifetime of the fish) for the four different estimates of ambient temperature. All these plots indicate the same tendency; a rather pronounced increase in mean length with temperature for ages 2-4. The mean length of age 1 does not seem to be related to temperature and for fish older than 5 year the material is very scanty. It is also noted (Figure 8) that the positive relation between length and temperature appears to decrease with age from age 2. Linear regressions between mean length at age and accumulated ambient temperature (not included in the paper) yields slopes between 1.5 and 2.5 cm per degree centigrade for agegroups 2 and 3. This would imply that a 2 year old cod which inhabits waters of 4 ^{0}C was 1.5-2.5 cm longer than the one that inhabits waters of 3 ^{0}C. As the average length of a 2 year old cod varies between 19 and 29cm (Table 3) the relative difference in length is 5-13 percent.

From analysis of seventeen North Atlantic cod stocks Brander (1994 and 1995). found an almost 30 percent increase in weight at age 4 for each degree increase in temperature. Since the relative change in length is approximately one third of the relative change in weight, Brander's finding corresponds to an increase in length of about 10 percent per degree in temperature, a result which is comparable to those appearing from Figure 8. Brander's studies also indicate that the significance of temperature on growth of cod decreased by age, as does the curves drawn (straight line imagined) in Figure 8.

In an attempt to increase the amount of data for the analyses made in Figure 8, mean values of length at age and mean ambient temperature back to 1978 were included. The results indicate an increase in length with ambient temperature of 1.1-1.2 cm per degree for age groups 2-5. They also indicate that after age 3 the effects of temperature on growth are small or negligible (parallel lines in Figure 9). The length increments the fish has gained at age 2-3 from higher ambient temperature are maintained at age 4-5 but no additional increments with temperature can be observed. The reduction in slopes with age is probably mainly an effect of fishing, which will remove the fastest growing specimens at an increasing rate from age 3 to age 5-6 when the 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.

A length difference of 1.2 cm per degree centigrade implies that a cod inhabiting waters of 5 ^{0}C is about 5 cm greater in length than one inhabiting waters of 1 ^{0}C. For 2 years olds (20-25cm mean length) the finding corresponds to 5-6 percent per degree in length and 15-20 percent per degree in weight, decreasing with age (size). This is considerably less than indicated from the data set 1988-1995 (Figure 8) and the figure of almost 30 percent per degree in weight for 4 year old cod as reported by Brander (1995).

For pelagically distributed 0-group cod (0-60 m depth) Loeng et al. (1995) observed faster growth during summer and greater mean length of the yearclasses in August in warm years than in cold, while Helle (1994) found no relation between mean lengths and temperature within a particular year. Our finding that the mean length of age 1 is not or poorly 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. 1996); both factors that may change the mean length-temperature relation of the yearclass prior to our observations in February. Also the estimated mean lengths of age 1 cod are uncertain due to length selective sampling.

In the present analysis we have used ambient temperatures for February. Due to the seasonal migration patterns of cod, these temperatures are probably close to the annual maxima (Ottersen *et al.*, 1996). The actual annual means of ambient temperature will probably be significantly lower than the values for February, particular for the older age groups (4-7 years), since these fishes feed in cold water areas during the summer-autumn season. Consequently also the differences in ambient temperatures between age groups as well as between years for each year class and thus the estimated slopes might be lower than if annual means had been used. The present analyses therefore most likely tend to underestimate the effect of temperature on growth.

Growth of Northeast Arctic cod is attempted estimated by a bioenergetic model

(Aijad, 1996), where temperature is an important variable. The temperatures used in the model so far are those which are used for estimating the consumption by cod. As shown by Ottersen *et al.* (1996) these are significantly higher for the period 1991-1995 than our estimates of ambient temperature. In order to test the model thoroughly for use in assessment, estimates of ambient temperature ought to be used as input, and the outputs from the model ought to be compared with observed growth.

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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 greater than 100 specimens per square nautical mile.

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

Table 2. Differences in mean length at age in western and eastern parts of the investigated area, 1988-1995. [L (West of 20 ^{0}E) - L (East of 35 ^{0}E)]. (-) indicate years without fish in eighter of these two areas

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7
1988	-	1.30	4.22	-	-	-	-
1989	-	-1.39	-2.17	0.17	2.65	6.70	-
1990	-	3.39	6.20	1.83	-	-	-
1991	-0.38	1.49	6.56	-1.72	-5.28	-3.79	-2.20
1992	-0.71	-0.47	4.93	3.31	1.37	1.41	-0.51
1993	-0.04	0.41	2.12	0.94	-0.43	-0.43	-2.42
1994	0.20	0.11	1.37	1.56	8.03	5.92	11.76
1995	-0.12	-0.30	2.87	0.21	1.22	3.10	-2.46
Total	-0.21	0.57	3.26	0.90	1.26	2.15	0.83

Table 3. Mean lengths at age by temperature and year. The two last columns show mean length at age and ambient temperature based on bottom temperature and swept area densities.

Year	Age	Length of fish within temperature intervals in cm (upper boundaries given)																		$\bar{L}$	$\overline{t_{amb}}$
		< -1	-0.5	0	0.5	1	1.5	2	2.5	3	3.5	4	4.5	5	5.5	6	6.5	7	>=7		
1988	1	-	-	-	-	-	-	-	15	-	-	13	-	-	-	-	-	-	-	15	2.95
1988	2	-	-	-	-	-	23	24	22	23	23	24	24	25	-	-	-	-	-	24	3.93
1988	3	-	-	-	-	-	31	29	30	29	29	30	30	31	-	36	-	-	-	30	3.45
1988	4	-	-	-	-	-	37	38	38	39	38	38	38	38	43	39	42	-	-	38	3.16
1988	5	-	-	-	-	-	45	46	48	46	48	47	47	46	51	51	51	-	-	47	3.61
1988	6	-	-	-	-	-	-	59	60	55	64	58	60	61	60	61	60	-	-	60	4.28
1988	7	-	-	-	-	-	-	-	74	-	77	75	76	77	76	74	72	-	-	75	4.25
1989	1	-	12	12	12	12	12	12	12	12	12	13	13	12	-	122	-	-	-	12	2.41
1989	2	-	-	29	27	26	26	25	26	26	26	26	26	25	26	22	24	-	-	26	2.80
1989	3	-	-	35	34	35	34	34	34	34	34	34	34	35	33	35		37	-	34	2.19
1989	4	-	-	40	40	40	40	41	39	40	40	40	41	42	41	43	43	43	-	40	1.93
1989	5	-	-	45	48	48	46	48	47	48	48	48	48	48	49	50	50	49	-	48	2.74
1989	6	-	-	51	54	53	53	55	55	57	56	57	57	57	58	59	60	59	-	57	3.89
1989	7	-	-	-	68	-	-	66	69	67	69	67	68	67	68	66	68	68	-	68	4.29
1990	1	12	13	12	-	13	13	14	15	14	15	15	14	13	13	-	12	-	-	14	2.52
1990	2	-	-	-	-	17	17	28	22	26	27	29	30	30	30	-	26	-	-	29	3.89
1990	3	-	-	-	-	-	-	-	38	37	37	38	38	39	39	41	41	43	-	39	4.51
1990	4	-	-	-	-	-	-	-	47	47	46	47	47	48	47	50	47	48	-	48	4.66
1990	5	-	-	-	-	-	-	-	55	54	54	54	54	54	55	56	55	55	-	55	4.88
1990	6	-	-	-	-	-	-	64	63	62	62	61	60	61	61	61	62	61	-	61	5.24
1990	7	-	-	-	-	-	-	-	69	69	68	69	70	68	69	69	70	69	-	69	5.49
1991	1	-	14	14	13	14	14	13	14	13	13	14	14	13	13	12	13	-	-	14	1.59
1991	2	-	20	18	18	21	25	24	26	27	28	31	31	32	30	27	26	25	-	27	2.59
1991	3	-	-	-	-	-	29	-	41	41	41	43	42	43	45	49	44	43	-	42	3.85
1991	4	-	-	-	-	-	-	-	53	52	52	52	53	52	53	53	51	51	-	52	4.40
1991	5	-	-	-	-	-	-	-	61	58	56	59	61	60	60	59	58	58	-	59	4.27
1991	6	-	-	-	74	-	-	-	69	67	65	67	68	68	68	67	67	67	-	68	4.52
1991	7	-	-	-	76	-	-	-	75	73	70	74	74	74	73	73	73	72	-	73	4.56
1992	1	-	-	13	13	13	13	13	14	13	13	13	13	13	13	13	-	-	-	13	2.42
1992	2	-	-	22	23	22	24	22	24	25	25	25	26	26	27	21	21	-	-	24	2.72
1992	3	-	-		-	41	41	41	39	41	41	40	43	43	43	43	44	-	-	41	3.50
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1992	5	-	-	-	-	-	59	61	61	60	60	60	61	59	61	61	61	-	-	60	4.35
1992	6	-	-	-	-	-	68	68	68	69	69	68	68	69	69	69	69	-	-	69	4.32
1992	7	-	-	-	-	-	-	76	77	76	77	76	75	77	77	77	77	-	-	77	4.42
1993	1		-	13	12	12	12	12	12	12	12	12	12	12	13	13	-	13	-	12	1.72
1993	2		-	20	21	21	20	20	22	22	24	23	23	22	20	25	23	26	-	21	1.52
1993	3	-	-	33	34	35	35	35	35	36-	-36	38	40	39	39	37	-	39	-	36	2.20
1993	4	-	-	-	49	49	47	47	48	50	50	52	52	53	54	51	53	52	-	51	3.34
1993	5	-	-	-	58	58	57	57	59	59	60	60	60	60	60	59	60	60	-	60	4.00
1993	6	-	-	-	72	75	-	67	66	70	69	70	70	70	69	70	70	70	-	70	4.04
1993	7	-	-	-	77	-	-	-	77	78	77	78	78	78	75	77	75	74	-	77	4.35
1994	1	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	-	-	-	12	1.13
1994	2	17	19	19	18	18	19	19	18	18	17	18	17	17	18	-	-	-	-	19	0.63
1994	3	27	26	28	30	31	31	33	34	33	33	34	37	37	35	-	-	-	-	31	1.03
1994	4	-	44	43	43	43	45	44	45	47	47	48	48	51	51	48	-	-	-	45	1.96
1994	5	-	52	51	52	51	52	52	53	57	57	58	58	61	60	63	-	-	-	55	2.64
1994	6	-	61	62	60	62	60	62	60	65	65	67	68	69	68	70	-	-	-	65	3.08
1994	7	-	-	-	76	-	71	74	71	72	73	75	76	79	78	-	-	-	-	74	3.10
1995	1	12	13	13	12	13	12	13	13	13	12	12	12	12	12	12	11	-	-	13	1.53
1995	2		18	17	20	19	17	20	19	19	21	23	21	21	21	20	20	-	-	19	1.49
1995	3	-	25	22	24	27	33	29	31	31	32	33	35	35	35	36		-	-	30	2.23
1995	4	-	-	-	40	35	44	42	42	41	43	43	45	45	44	44	43	-	-	43	2.72
1995	5	-	-	-	-	-	53	52	54	54	55	54	55	55	55	55	55	-	-	55	3.09
1995	6	-	-	-	-	-	61	60	66	65	64	64	65	64	63	64	65		-	63	3.45
1995	7	-	-	-	-	-	72	75	76	76	77	78	77	76	76	77	77	-	-	76	3.64

Table 4. Results of linear regression of mean length at age (L) on ambient temperature (T) [L=intercept+slope*T] all data 1988-1995. SE is standard error, R is correlation coefficient.

Age (year)	1	2	3	4	5	6	7
Intercept (cm)	12.7	19.3	28.6	42.4	50.6	59.1	74.6
SE Intercept	0.2	0.8	0.4	0.4	0.5	0.4	0.8
Slope (cm/degree)	-0.05	1.06	1.93	0.99	0.84	0.65	-0.50
SE Slope	0.04	0.20	0.10	0.10	0.11	0.10	0.18
R^2	0.09	0.64	0.96	0.88	0.80	0.88	0.42
Weighted Slope	-0.02	0.26	0.97	0.57	0.52	0.36	0.04

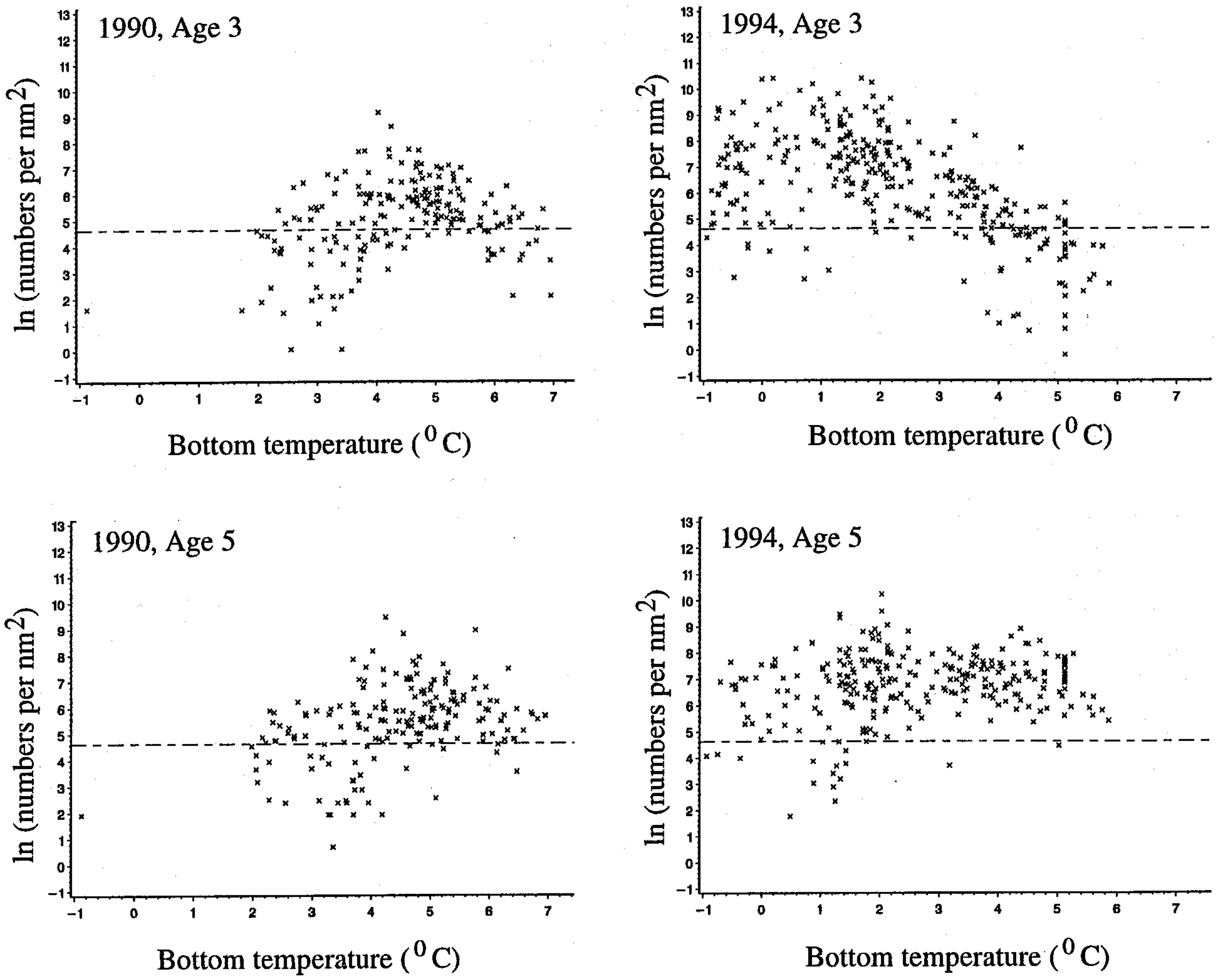

Figure 1. The distribution of density estimates at stations (natural logarithm of numbers per square nautical mile) for the 3 (upper) and 5 years old cod (lower) in 1990 and 1994, within temperature intervals. Dotted line indicates the level of 100 fish per nautical mile squared.

Table 5. Results of linear regression of mean length at age (L) on accumulated ambient temperature (T) [L=intercept+slope*T] all data 1978-1995. SE is standard error, R is correlation coefficient.

Age (year)	1	2	3	4	5	6	7
Intercept (cm)	12.3	18.6	26.8	32.9	39.1	45.9	55.5
SE Intercept	0.9	1.1	2.1	3.0	4.1	5.7	9.5
Slope (cm/degree)	0.83	1.23	1.14	1.18	1.07	0.96	0.82
SE Slope	0.39	0.23	0.27	0.26	0.26	0.29	0.39
R^2	0.23	0.64	0.54	0.57	0.54	0.47	0.27

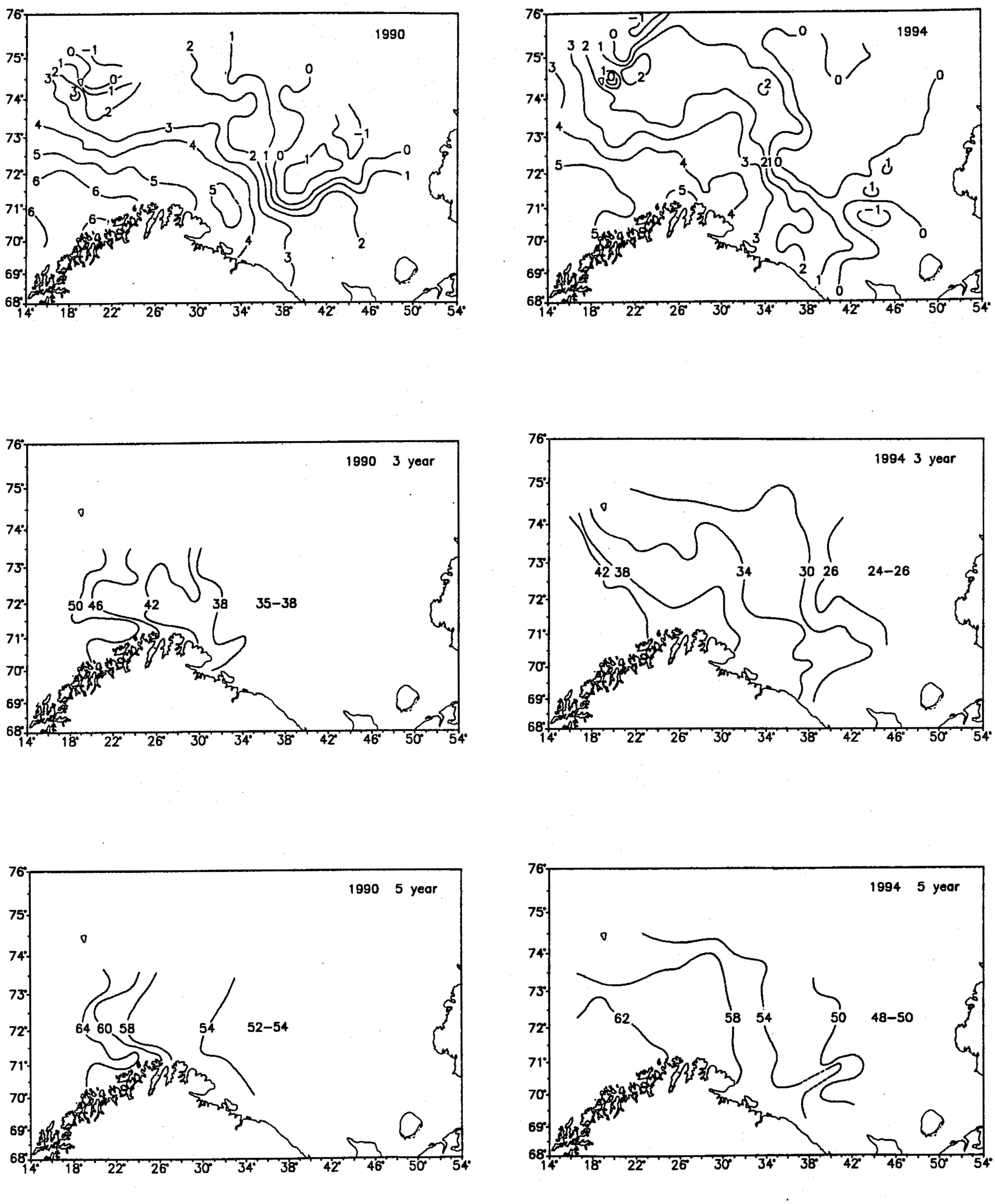

Figure 2. Horizontal distribution of temperature (^{0}C) at bottom (upper panel) and length (cm) at age of 3 (middle panel) and 5 years old cod (lower panel) in 1990 and 1994. Isolines are drawn from calculations of bottom temperature and mean lengths at age at trawl stations.

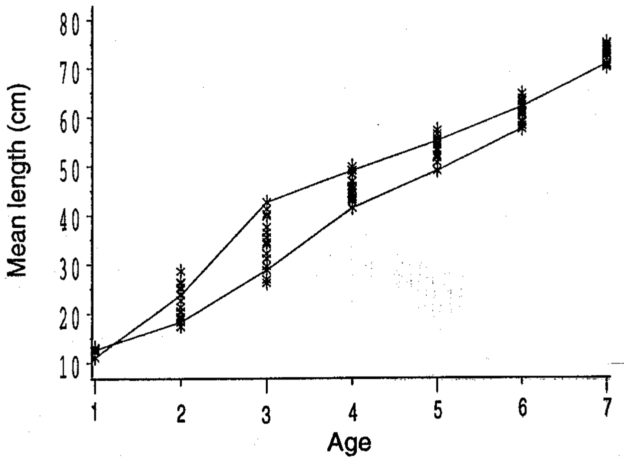

Figure 3. Mean length at age at temperatures ranging from -1 to 7 ^{0}C at intervals of 0.5 ^{0}C, combined for all years from 1988-1995. Lines are drawn for 0 ^{0}C and 6.5 ^{0}C.

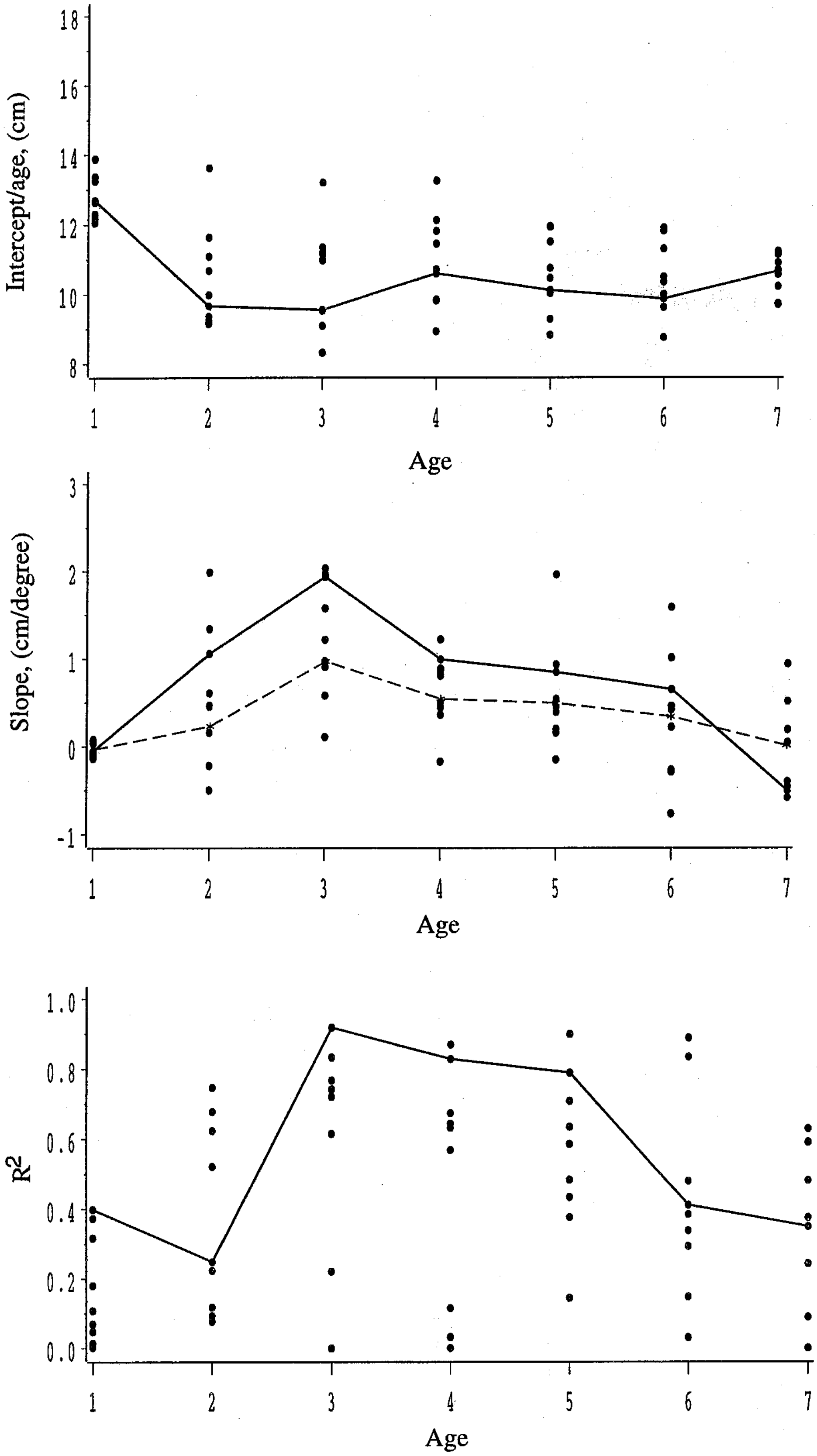

Figure 4. Results of linear regressions of mean length at age on ambient temperature (intercepts, slopes and correlation coefficients. Full lines are results when combining data from all years in one regression. Dotted line shows the results for weighted means of slope for each particular year.

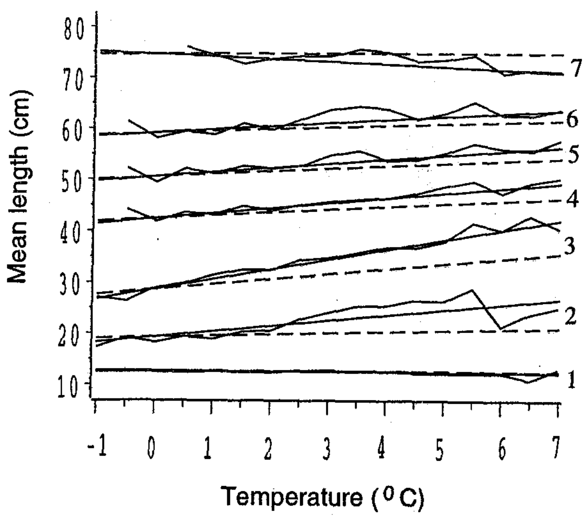

Figure 5. Relationships of length at age and temperature for each agegroup. Full lines are based on results from linear regressions when data from all years were combined, while dotted lines are based on weighted means of statistics from regressions for each particular year. Curved lines represents estimated mean length at age within each temperature interval. Numbers to the right indicate age group.

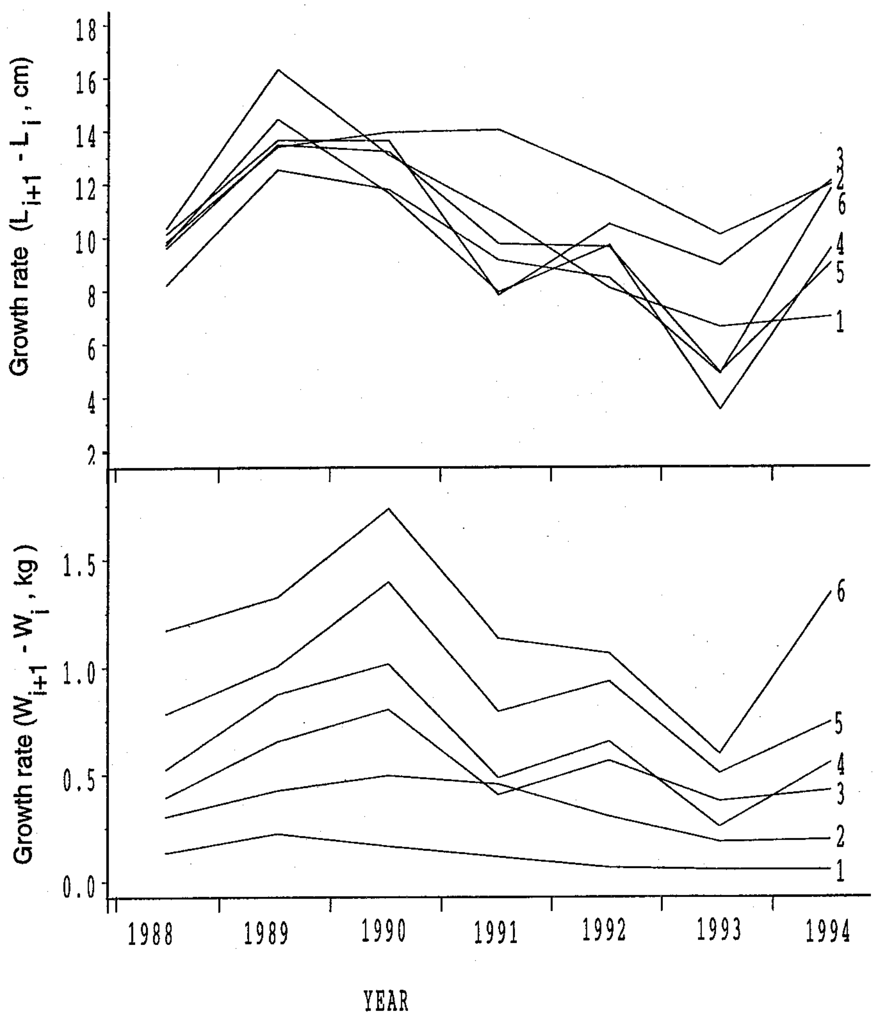

Figure 6. Absolute annual growth rate in length and weigth. Numbers to the right indicate age group.

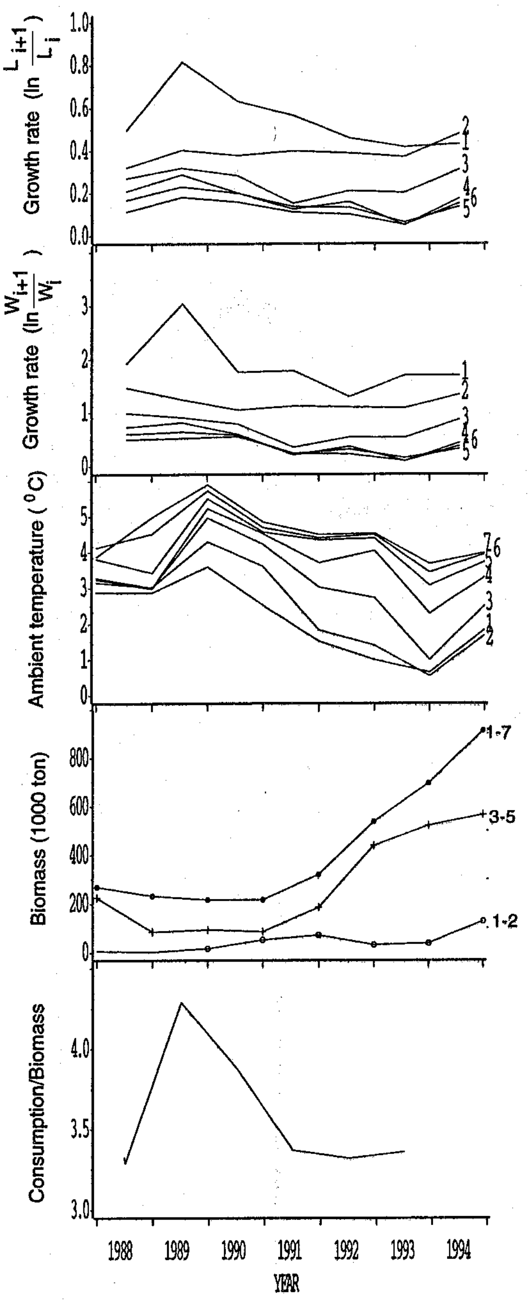

Figure 7. Specific annual growth rates in length and weight compared with mean ambient temperature, biomass and consumption/biomass ratio. Numbers to the right indicate age group.

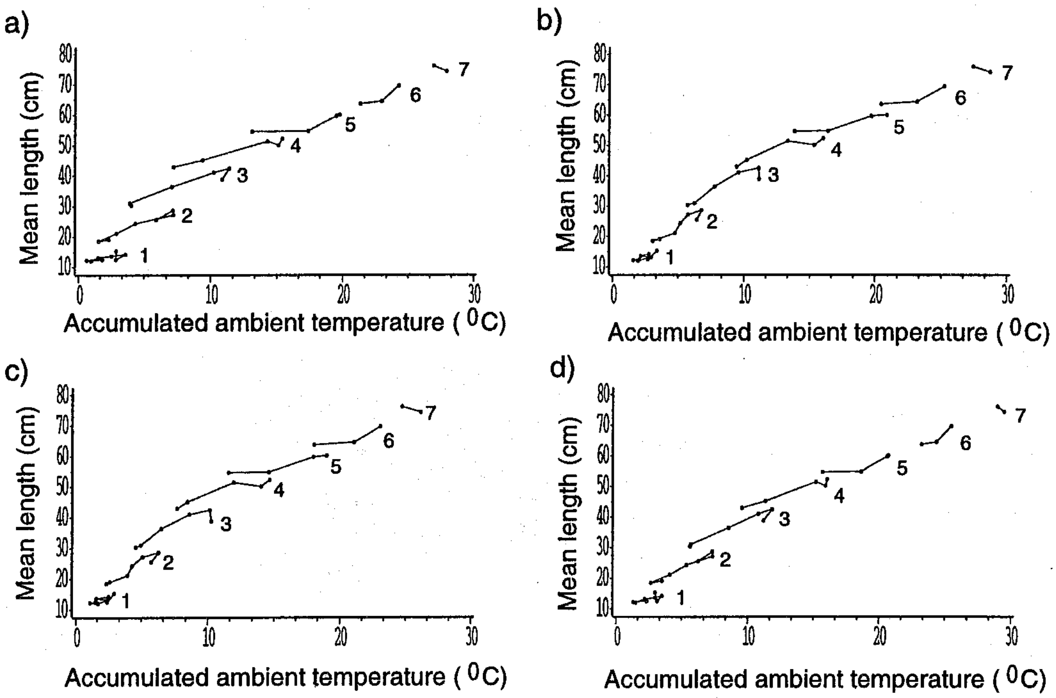

Figure 8. Mean length at age in relation to accumulated ambient temperature for various combinations of density estimates and temperature, 1988-1995. a) acoustic density and bottom temperature, b) acoustic density and temperature from 100m depth -bottom, c) swept area density and bottom temperature, d) swept area density and temperature from 100m depth -bottom. Numbers to the right indicate age group.

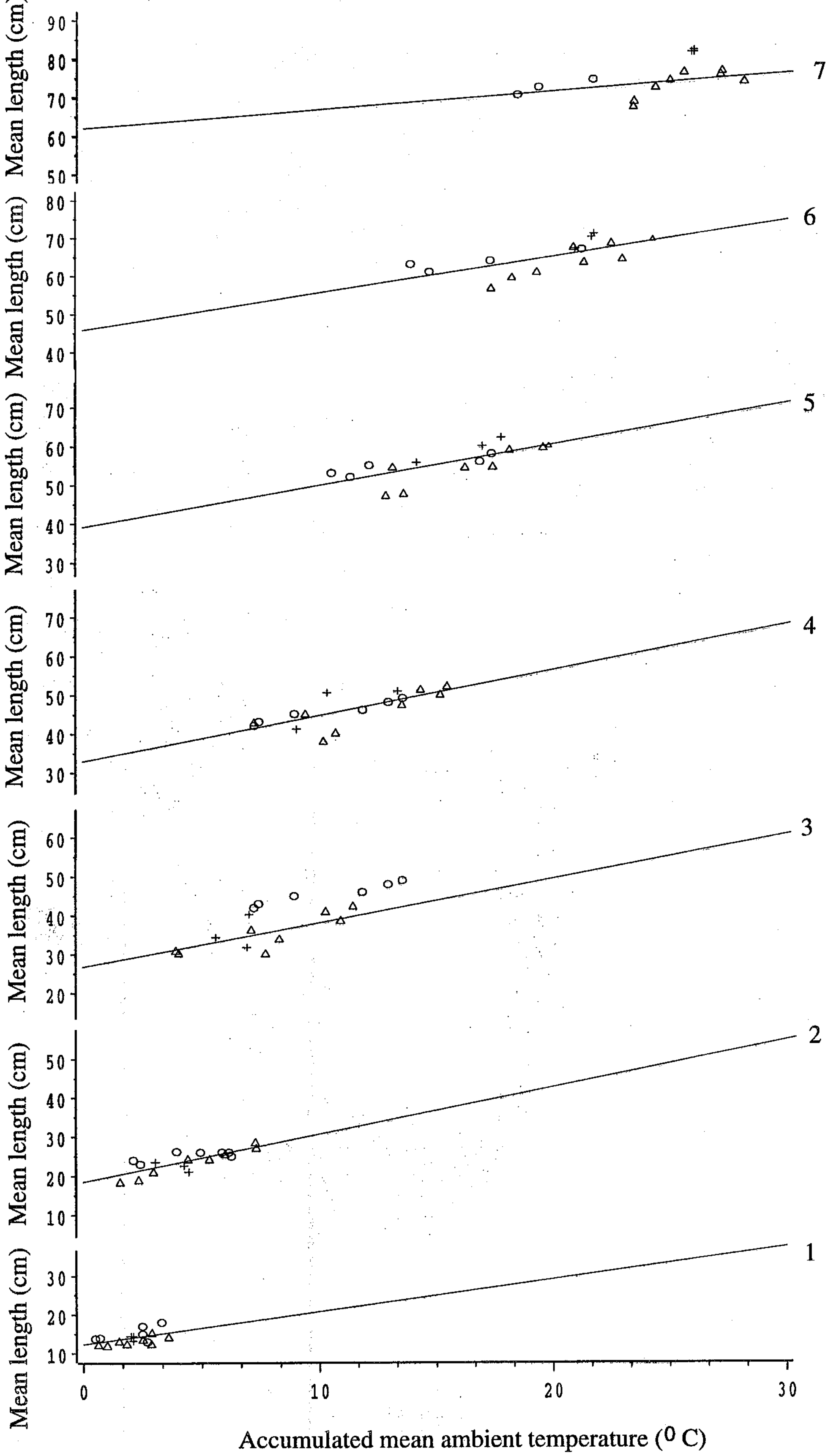

Figure 9. Mean length at age in relation to accumulated ambient temperature based on acoustic estimates and bottom temperature, 1978-1995. Triangles indicate data from 1988-1995, circles indicate data from 1978-1995 and plus indicate data from 1985-1987.