

GROWTH OF THE NORTHEAST ARCTIC COD (GADUS MORHUA L.) WITH  
SPECIAL REFERENCE TO LONG-TERM CHANGES AND THE EFFECTS OF  
VARIATIONS IN STOCK ABUNDANCE AND TEMPERATURE ON GROWTH

**ABSTRACT**

An analysis of growth in length of immature Northeast Arctic cod between 1953 and 1988 showed marked short-term variation, and a significant long-term increase in length at age was found for age groups 5 to 8. Clear geographic differences in length at age were found, making the estimation of population means critically dependent on the sampling strategy. Insignificant differences in growth between sexes were observed up to age 5, but matures of an age group were generally larger than immatures. Growth of cod was found to be linear, with an average growth rate of approximately 10 cm/year after age 2. Year classes with above average length at age 2 maintained an above average length at least till age 6. Synchrony in the ranking of years according to growth rate was found for age groups 3 and older. No significant density-dependent growth response to short-term fluctuations in stock abundance was detected, but an overall increase in length at age between 1953 and 1988 probably indicates a long-term response to the reduction in stock size. No statistically significant relationships were found between growth rate and temperature indices or between growth rate and capelin biomass.

## INTRODUCTION

Fishes are characterized by having extremely plastic and consequently highly variable growth (Weatherley 1972). Our understanding of the factors controlling growth rate and especially the ways these factors interact is, however, still very incomplete. Moreover, some of the ecological parameters known to influence growth, e.g. available abundance of prey, are extremely difficult to estimate in the field. As a consequence efforts to model temporal growth variations have so far met with moderate success.

Studies of wild stocks have generally focused on the ways stock abundance and temperature influence growth. An inverse relation between growth and stock abundance has been shown for several species, both demersal and pelagic (e.g. Beverton and Holt 1957, LeCren 1958, Raitt 1968, Lett and Doubleday 1978, Jones 1979, Houghton and Flatman 1981). For others no significant correlation has been found (e.g. Hempel 1957, Daan 1974, Bannister 1978). An inverse relation suggests that growth is limited by suitable food and a dependency of growth rate on food consumption has been clearly documented experimentally (e.g. Waiwood 1978, Brett 1979, Jobling 1982). However, abundance of prey may vary as much and sometimes in parallel with fluctuations in predator abundance and thereby obscure a possible density-dependent growth regulatory mechanism. Growth rate generally increases with increasing water temperature until an optimum temperature is reached, provided an adequate amount of food is available. The effect

of temperature on growth rate has been thoroughly documented by laboratory experiments (Saunders 1963, Waiwood 1978, Brett 1979, Holdway and Beamish 1984) and also substantiated by field data (Hansen 1949, Powles 1958, Taylor 1958, Fleming 1960).

For the Northeast Arctic cod (Gadus morhua L.) several authors have claimed or suggested that growth is density-dependent (Rollefsen 1953, Sætersdal and Cadima 1960, Ponomarenko 1967, Cushing and Horwood 1977). Dementyeva and Mankevich (1965) and Nakken and Raknes (1987) claimed to observe a temperature dependency of growth. The studies referring to density-dependent growth as well as that by Nakken and Raknes (1987) are, however, flawed by the use of length as a synonym for growth rate, while the concordance between length and summed temperature observed by Dementyeva and Mankevich (1965) was questioned by Ponomarenko (1967).

The impact of variations in temperature and stock size on growth changes of the Northeast Arctic cod is hence not sufficiently documented. Information on growth pattern and temporal growth changes is also scanty, despite an extensive research effort on cod since the beginning of this century. The objective of this study was therefore to analyse growth pattern and growth changes of the Northeast Arctic cod based on the samples collected by Norwegian research vessels since the late 1940s. Of special interest were indications of density-dependent growth or a dependency of growth rate on sea temperature. An attempt was also made to relate growth

rate to abundance of capelin (Mallotus villosus), a principal prey species of cod.

## **MATERIAL AND METHODS**

### Biological data

Since 1946 bottom trawl samples of Northeast Arctic cod have been collected in the Barents Sea by the Institute of Marine Research, Bergen. Before 1975 the number of samples was small and the geographical distribution as well as time of sampling highly variable among years. Since 1981 a stratified random trawl survey has been conducted annually in winter in the southern Barents Sea to assess the abundance of young cod and haddock (Dalen et al. 1982, Dalen et al. 1983, Dalen et al. 1984, Hysten et al. 1985, Hysten et al. 1986, Godø et al. 1987, Hysten et al. 1988).

Before 1974 trawls with varying codend mesh sizes were used. For some years information on actual codend mesh size used is lacking, and for these a mesh size of 135 mm was assumed. From 1974 onwards shrimp trawl has been used as the standard trawl by the research vessels. Selectivity experiments indicate that with a 135 mm mesh size, cod less than 55-60 cm are affected by mesh selection (Hysten 1966, Hysten 1967, Anon. 1971).

Individual weights were recorded on the winter surveys in the years 1984 to 1986 and in 1988. A small number of weight

measurements were also collected in 1946, 1953, 1972 and 1973, but in different seasons. Measurements of length refer to total length (cm) and of weight to ungutted weight (grams). Ageing was made from sagittal otoliths (Rollefsen 1933, Williams and Bedford 1974). Only observations for which both length and age had been determined were included in the analysis. Cod classified as coastal cod on basis of the otolith growth pattern (Rollefsen 1933) were excluded from the analyses.

The study of long-term changes in length at age and variations in growth related to stock size and temperature was restricted to immature fish (primarily age groups 2-7). These age groups are also the more abundant in the collected material. Only data collected in the period January to April (available from 1953 onwards) were included in the analysis. For this period all data from the area shown in Fig. 1 were pooled and considered as a random sample from the population. Data from other months were only used for the study of seasonal growth.

#### Data on stock abundance

Estimates of abundance for the period 1964 to 1987 were obtained from the report of the ICES Arctic Fisheries Working Group (Anon. 1988). Data for the years 1953 to 1963 were calculated by Virtual Population Analysis (VPA) using catch at age data from the ICES database and the estimated fishing mortality rates in the 1988 report (op. cit.) as starting values for the iteration. Estimated stock sizes are

given in Appendix I and refer to abundance at 1 January each year. Unless otherwise stated, the arithmetic mean of stock abundance at 1 January and 31 December was taken as an annual average and used in the analysis of growth in relation to stock size.

#### Temperature data

Observations for the Kola section (along the meridian E 33°30' and between N 70°30' and N 72°30') were used as a temperature index for the Barents Sea. For each month an average temperature for the 0-200 m depth interval was available. These observations were collected by the Knipovich Polar Research Institute of Marine Fisheries and Oceanography in Murmansk, USSR and made available by the Institute of Marine Research, Bergen.

#### Calculation of growth rate

The growth rate of an age group was defined as the length increment across one calendar year:

$$\text{growth rate}(i) = l(i+1) - l(i) \quad (1)$$

where  $l(i)$  and  $l(i+1)$  are the length of the same year class when of age  $i$  and  $i+1$  respectively.

For a comparison of growth rates between years a correction for differences in initial length is usually necessary as growth rate itself is a function of length (Iles 1967). If the growth pattern is linear and growth rate is defined by Eq. 1, no correction is needed.

## RESULTS

### INTRA-ANNUAL VARIATION IN LENGTH AT AGE

#### Geographical variations

To analyse geographical variation in length at age, the area covered by the winter trawl survey was arbitrarily divided into three subareas (Fig. 1) and mean lengths were calculated for age groups 2 to 6 for each subarea (Table 1).

Generally, mean length at age increased from the eastern (I) to the western (III) subarea. The difference in mean length at age between areas varied appreciably between years, the largest observed difference (for means based on a minimum of 10 observations) between subareas I and III was 7 cm (3 year olds in 1985). A two-way ANOVA (with equal cell weights) of length at age with factors area and year showed significant differences between subareas for age 2 (Table 2). For age groups 3 to 6 a significant interaction term was found and no conclusion can therefore be drawn regarding the significance of differences between areas for these age groups.

However, the mean sum of squares indicated that the between-year variation was dominating relative to the between-area variation. Nevertheless, a one-way ANOVA showed significant differences between subareas, more frequently for the 3 to 5 year olds than for the 6 year olds, for which significant differences were found in 2 out of 6 years only (Table 3). Age groups 5 and 6 were poorly represented in the samples from subarea I, and a comparison for these two age groups was made for subareas II and III only.



### Sexual differences

A two-way ANOVA for length at age for the period 1974 to 1988 showed no significant difference between females and males of ages 2 to 5 years, but significant differences were found for the 6 and 7 year olds (Table 4). Males and females of these age groups differed, however, by less than 2 cm and the values of the mean squares indicated that the inter-annual variation in length at age was much larger than variation between sexes.

### Differences between matures and immatures

The number of mature fish in the trawl catches was generally small, especially before the late 1970s. The analysis of differences in length at age between mature and immature fish was therefore confined to age groups 5 to 7 which had the highest number of mature specimens (Table 5). The results of a two-way ANOVA showed no significant effect of maturation on length at age for the 7 year olds (Table 6). For the 5 and 6 year old fish a weak, but significant interaction was found. The mean sum of squares for the year factor was approximately three times that for the stage of maturity factor in the ANOVA and again indicated the greater importance of year-to-year variations compared with differences between mature and immature. Analyses on an annual basis showed, however, that mature fish were generally significantly larger than immatures (Table 5). Extreme differences observed between mean length at age of mature and immature fish were of the order 5 to 6 cm.

### Seasonal growth pattern

The data did not permit a detailed study of seasonal growth, but for the years 1982 to 1984 the number and temporal distribution of samples were sufficient to establish a seasonal growth curve (Fig. 2). Monthly mean lengths at age were computed and indicated that the larger part of the annual growth in length took place between May and November. The seasonal growth seemed to be synchronized with the period of increasing water temperatures in the Barents Sea (Fig. 2).

### INTER-ANNUAL VARIATIONS IN LENGTH AT AGE

#### Long-term changes

The data for mean length at age showed more pronounced short-term than long-term variation in the period studied (Fig. 3a). The two most pronounced short-term changes in mean length at age were observed in the mid 1960s and in the mid 1980s. A significant overall increase in length at age across the period 1953 to 1988 was found for age groups 5 to 8 (Table 7). No significant trend was found for age groups 3 and 4 for the same years. Based on data from the period 1968 to 1988 (unbiased by mesh selection) no significant overall trend was found for any of the age groups 2 to 7 (Table 8). Data from the spring fishery along the coast of Finnmark (the "Loddetorsk" fishery) showed a similar overall change in mean length at age across the period 1953 to 1988 as indicated by the trawl data and the same short-term trends were visible (Fig. 3b). Significant increase in length at

age was found for all age groups analysed (4 to 7) (Table 7).

#### Growth pattern

The data also showed that growth in length of the Northeast Arctic cod was remarkably linear within the age range covered (Fig. 4). Inclusion of data from the spawning fishery at Lofoten to cover a wider age range did not change this growth pattern. Linear regression of mean length against age of a year class accounted for more than 95% of the variation in length (year classes 1971 to 1981, age range 2 to 10 years).

Growth curves for the year classes 1971 to 1981 appeared to be almost parallel (Fig.3a), indicating that differences in length at age were established mainly before the age of 2 years. An analysis of covariance showed that average annual growth rates of these year classes were significantly different ( $F= 4.35$ ,  $df= 10,40$ ;  $p < 0.01$ ). However, the ranking of length at age of the same year classes agreed well (Kendall's coefficient of concordance,  $W= 0.61$ ;  $p < 0.01$  (Sokal and Rohlf 1981)). Cod grew on average 10.3 cm/year after age 2, the range was 9.1 to 11.9 cm/year (year classes 1971 to 1981).

The ranking of years according to growth was significantly correlated for age groups 3 to 6 (Kendall's  $W= 0.82$ ,  $p < 0.01$ ,  $n=14$ ; Table 9 and 10). Ranking of years was however not

significantly correlated between age 2 and any of the ages 3 to 6. The concordance generally increased with increasing age and decreasing age difference.

#### CHANGES IN THE LENGTH-WEIGHT RELATIONSHIP

Based on the data from 1984 to 1986 and from 1988, the length-weight relationship ( $W = aL^b$ ) was calculated for the immature fish. The b-parameter was significantly lower in 1986 and 1988 than in 1984 and 1985 (Table 11). The data showed that median weight at length was reduced by approximately 20% from 1984 to 1988 (Fig. 5). Fish below 25-30 cm showed a less marked reduction in weight at length, most clearly seen in 1988.

#### GROWTH RELATED TO STOCK SIZE AND TEMPERATURE

Scatter plots of growth rate of an age group versus the mean annual abundance of the same age group revealed no close covariance for the years 1968 to 1987 (Fig. 6). Correlation analyses generally indicated an inverse relationship between growth rate and year class abundance, but no statistically significant relationship was found (Table 12). Other measures of stock abundance (inclusion of the preceding and following year class and total stock abundance, i.e. age 3 and older), generally resulted in lower values of the correlation coefficients (Table 12). A tendency towards increasing dependency on abundance with increasing age is seen, but only one significant correlation was found; between the growth rate of 6 year old fish and the stock abundance of 5

to 7 year olds. Moreover, when data for the period 1953 to 1987 were analysed, the inverse relationship between stock abundance and growth rate became even less clear.

An attempt was made to correlate growth rate with two indices of water temperature: sum of monthly mean temperatures in the Kola section across the growth season (defined as the months May to October according to the seasonal growth curve) and across the whole year. No close functional relationship was indicated by scatter plots (Fig. 7). Growth was positively correlated with both indices, but the highest covariance was usually seen when using summed temperature across the growth season (Table 13). Only for the 3 year olds was the correlation significant. Disregarding the 2 year olds, the values of the correlation coefficient generally decreased with increasing age, indicating less effect of temperature on growth as the fish grew older.

The cumulative effect of temperature across the life of a year class was studied by plotting length at age against the summed monthly mean temperatures from hatching to time when caught (Fig. 8). For shorter periods the trend in temperature and length at age was concordant (e.g. the early 1980s), but for others it diverged. No significant correlation was found between the length at age and the summed temperature for age groups 3 to 5 years, but for the 6 and 7 year old fish a significant negative correlation was observed (Table 14). No overall trend in mean annual temperature in the

Kola section was detected between 1953 and 1988 (linear regression coefficient  $b = -0.013$ ,  $p > 0.10$ )

#### GROWTH RELATED TO CAPELIN STOCK SIZE

An attempt was made to correlate the growth rate of cod with the spawning stock biomass of capelin. Estimated stock sizes of capelin were reported by Anon. (1989). No statistically significant relationship was found based on the available data from 1974 to 1988 (Table 15). The highest correlation coefficient was obtained for the 5 year olds ( $r = 0.365$ ,  $n = 14$ ).

### DISCUSSION

#### EVALUATION OF DATA

The analysis of growth of cod in this paper was based on the four implicit assumptions

- a) that the computed mean length at age is an unbiased estimate of the population mean length at age;
- b) that fish are correctly aged;
- c) that variations in temperature in the Kola section reflect variations in the environment where the fish live;
- d) that the VPA-estimates reflect variations in stock abundance.

Clearly, not all of these assumption are fully valid. For the interpretation of the results it is therefore important

to evaluate the sources, direction and extent of bias in the data.

The estimates of mean length at age

Length at age data collected before 1974 are likely to be biased by codend mesh selectivity for age groups younger than 5 years. The samples from 1974 onwards were collected with a shrimp trawl as the sampling gear and are therefore not biased by codend selectivity for length. Recent experiments have, however, demonstrated a considerable length dependent escape under the trawl (Engås and Godø 1989), thus making the estimated mean lengths at age biased upwards. Fish smaller than 70 cm are affected by this type of gear selectivity, although it operates more strongly on the the young cod (age groups 1 to 3) (op. cit.).

Moreover, the observed geographical differences in mean length at age of cod between the eastern and western part of the distributional area make the estimates of mean length of an age group strongly dependent on the geographical distribution of the samples. The smallest fish of an age group are generally found further east than the larger specimens. A disproportionate sampling intensity in the eastern areas will therefore likely bias length at age downwards.

To study inter-annual variation in length at age it might therefore seem more appropriate to restrict the analysis to data from a smaller subarea to avoid the possibility of confounding the between-area and between-year variance in

length at age. East-west displacements of the stock as a response to changes in the hydrographical regime in the Barents Sea have been clearly demonstrated (Midttun 1981) and the significant interaction between area and year in the two-way ANOVA is probably a result of year-to-year variations in the spatial distribution of cod. As size of an age group also shows a longitudinal cline, displacement of the stock will most likely change the mean length at age within a subarea. Hence, if estimates of mean length at age were based on samples from a geographical area smaller than the main area of distribution, the effect of displacement of the stock may intensify or reduce year-to-year variation.

Theoretically, even with a constant population mean length at age, fluctuations in estimated values may be created by this effect. Hence, the most appropriate approach would be to estimate means for smaller strata and then weigh by the proportion of fish in each stratum before calculating the population mean length at age. However, but such information is only available from 1981 onwards.

Sampling effort as well as geographical distribution of samples varied appreciably between years. To establish a time-series across years it was therefore decided to pool data from the whole distributional area of the immature stock in the Barents Sea (Fig. 1). It was also sometimes necessary to compare data collected at different times of the year. To minimize bias due to the intra-annual growth, only data collected between January and April, when the growth rate is low (Fig. 2), were included in the analysis.



By pooling samples, the variance of estimates of mean length at age was most likely underestimated.

Summing up, the estimated mean lengths at age are likely biased, both by gear selectivity and not least by the geographical distribution of samples. The ANOVA nevertheless demonstrated that for the marked changes in length at age observed between 1983 and 1988, the between-year variance was considerably larger than that due to geographical differences within the distributional area. The more pronounced inter-annual changes in length at age are therefore assumed to be real, while smaller changes may be artifacts.

#### Ageing

Age determinations of cod are generally considered accurate. An investigation of the precision of ageing nevertheless showed that as much as 1/3 of the determinations differed between first and second reading, however, 90% of these by one year only (O.S. Kjesbu, Inst. Marine Research, Bergen; pers. comm.). As length of the fish was known to the person reading the otoliths, smoothing of growth changes between years may have happened (Williams and Bedford 1974; Sætersdal and Loeng 1987). All otoliths had been broken for age determination and no attempt was therefore made to back-calculate length at age from otoliths. In cross sections from broken otoliths the size of the rings depends critically on the location of the break (Williams and Bedford 1974).

#### Temperature data

The variations in temperature in the Kola section have been shown to reflect well the actual variations in temperature in the overwintering area of age groups 2 to 8 (Nakken and Raknes 1978). During feeding migration in summer cod may be found in cold water masses in frontal areas (Beverton and Lee 1957). Thus, temperature variations in the Kola section probably reflect variations in the temperature experienced by the cod less accurately during the feeding season than in winter.

#### Stock abundance measures

The stock abundance measures based on VPA were estimated for the total stock of Northeast Arctic cod. Consequently, also the part of the stock in the Bear Island and Spitzbergen area was included. However, only a smaller fraction (varying between 5 and 25%) of the stock is found in these waters (for the years 1982 to 1985 less than 5% according to Hylen and Nakken (1982, 1983, 1984, 1985)), and VPA numbers can probably be used for the stock in the Barents Sea without introducing major bias. The accuracy of the VPA numbers are difficult to assess, but they were assumed to be superior to catch per unit effort data and acoustic estimates. An over-estimation of year classes adjacent to exceptionally strong ones as a result of incorrect ageing has, however, been suggested (Sætersdal and Loeng 1987).

## EVALUATION OF THE RESULTS

## Growth patterns

The seasonal growth pattern is difficult to determine from field data because of sampling errors (Daan 1974, Lett 1978). In this study the number of monthly mean values as well as the sample sizes were small. The exact shape of the seasonal curve is consequently uncertain. Nevertheless, the consistency of the seasonal length changes for the three years suggest that the described intra-annual pattern may be real. Moreover, the existence of a seasonal growth pattern has been documented by laboratory experiments (Waiwood 1978, Hall 1989), and also indicated by field data (Hawkins *et al.* 1985), although the results are somewhat inconclusive (Dannevig 1933, Daan 1974). The synchrony between increasing temperatures and growth in length seen in Fig. 2 does not necessarily reflect a causal relationship, as indicated by the experiments by Waiwood (1978). During the feeding season cod migrates eastwards and may enter water masses of low temperatures (Beverton and Lee 1965). The temperatures in the Kola section may consequently not reflect the actual temperatures during the feeding season and it is unlikely that the seasonal growth is solely a result of increased metabolic rates caused by higher water temperatures.

Since linear regression fitted the growth data well and there were no indications of asymptotic growth within the age range 2 to 10 years, other growth models were not used. No conclusion can be made about growth beyond the age of 10-

12 years, as fish of these ages are rare in the samples. It is noteworthy that no change in growth pattern was observed at the onset of sexual maturity, suggesting that enough energy is available to fill the requirements of both somatic growth and gonadal development. It has been hypothesized that the growth pattern of cod is a result of its ability to gradually utilize larger prey as it grows bigger (Jones 1989). A linear growth pattern is however not unique for cod in the Barents Sea, it has also been found for cod in the Northwest Atlantic (Beacham 1982) and for Greenland halibut (Reinhardtius hippoglossoides) (Bowering 1978).

Growth conditions of cod were found to be similar for age groups 3 to 6 in the same year, but no significant correlation was found between the 2 year old cod and the older age groups. This observation is probably a result of the change in diet with length of the cod. Fish smaller than 20 cm feed mostly on crustaceans, while bigger cod are more piscivorous (Mehl 1989). The relative reduction in weight at length between 1984 and 1988 was also almost uniform for cod between 35 and 75 cm, but less pronounced for the smaller cod (20-30 cm). Thus, feeding conditions were poor for the size groups largely dependent on fish prey, while the size groups that feed on crustaceans suffered no shortage of prey. A visual inspection of the growth rates showed small differences between some of the years. The ranking of years is consequently sensitive even to small changes in the estimated values of growth rates. Nevertheless, years with

exceptional growth for all of the age groups 2 to 6 was discernible (Table 9), notably 1984 and 1987.

#### Growth related to stock abundance

The indications of a clear relationship between growth and the size of the cod stock in the Barents Sea were vague. Although negative correlation coefficients were found between growth rate and stock abundance, they were generally not significantly different from zero. However, the pronounced reduction in growth rate and especially in weight at length from 1984 to 1987 clearly demonstrated poor feeding conditions for the cod in these years. Although the two comparatively strong year classes 1983 and 1984 recruited to the stock in these years, the stock of cod was nevertheless small compared to previous levels. However, the stock of capelin, one of the major prey items for cod, collapsed in 1985/1986, probably due to a too high fishing mortality and increased predation pressure by cod (Hamre 1988). In the period 1974 to 1982 stock size of cod was generally low and those of the major prey species, capelin and shrimp (Pandalus borealis), abundant. That may explain why no significant correlation was found between stock abundance and growth rate for the years studied.

A lack of indications of density-dependent growth (generally interpreted as a negative correlation between stock abundance and growth rate) may have several explanations. First, the results presented here showed clearly the difficulties

in estimating population mean lengths at age and consequently also growth rates. With an inadequate sampling strategy, it is likely that such errors account for much of the unexplained variation in growth rate as a function of stock size. Second, the abundance of prey populations also show large inter-annual fluctuations. If abundance of prey and predators are positively correlated, the result may be a lack of indications of density-dependent growth. A positive correlation between year class strength of several species was found by Dragesund (1971). Third, competition for food is dependent on the number of fish per unit area. The northern boundary for the distribution of cod is found in the Barents Sea, and the area of distribution is strongly affected by hydrographical conditions. In years with a high inflow of Atlantic water, temperature in the eastern Barents Sea increases and so does the potential feeding area for the cod. With the same stock size in a cold and a warm year, the density of fish, and therefore the competition for food, can consequently be very different. Fourth, the stock size of cod has been low in the period studied compared to the unexploited stock. This may also explain the lack of a significant density-dependent response to the observed variations in stock size. Density-dependent responses may only be of importance at higher stock sizes (Jones 1989).

The results also indicated that differences in length at age between year classes to a large extent were established before the age of 2 years. Hubold (1978) similarly observed that herring with an above average length at age 1 generally

maintained an above average length at age throughout their lives. These observations illustrate the methodological problem of using a positive correlation between length at age and a measure of stock abundance as an indication of density-dependent growth, as size as such does not give information on growth in individual years (Lett 1978, Sinclair *et al.* 1982). The investigations suggesting density-dependent growth in the Northeast Arctic cod (i.e. Rollefsen 1953, Ponomarenko 1967, Cushing and Horwood 1981) are, however, based on an analysis of length at age versus stock abundance, and the results are therefore invalid as indications of density-dependent growth. The fact that differences in length at age are established already at the age of 2 years, suggests that intra-specific competition is rather unimportant for cod older than 2 years and that a density-dependent growth response to changes in stock size is weak or non-existent.

#### Growth related to temperature

The apparent lack of a significant temperature effect on growth of the Northeast Arctic cod is probably the result of a discrepancy between temperature variations in the Kola section and those actually experienced by the cod. Except for the youngest cod, the fish may actively select its ambient temperature by east-west migration, and during feeding season cod migrates north- and eastwards. Moreover, the migratory behaviour increases with age. The decreasing value of the correlation coefficients between growth rate and

temperature with increasing age of the cod may therefore have a simple biological explanation. A close correlation between variance in growth rate and temperature fluctuations in the Kola section is, however, not to be expected.

The optimum temperature for growth of Northeast Arctic cod is higher than the temperatures observed in the Barents Sea (Godø and Moksness 1987, Jobling 1988). It is therefore suggested that the significant negative correlation between length at age and summed life span temperature for the 6 and 7 year old cod is either an artifact or alternatively a secondary response to temperature fluctuations. The relatively close correlation ( $r=0.71$ ) found by Dementyeva and Mankevich (1965) between length and summed temperature across the feeding seasons, does consequently not seem to be valid for a longer time period. Moreover, the apparent functional relationship between length and temperature found by Nakken and Raknes (1987) does not demonstrate a correlation between growth and temperature, simply that larger fish are found in warmer water during winter.

#### Long-term changes in length at age

Significant changes in lengths at age were observed across the period 1953 to 1988 based on both the data from the trawl surveys and the data from the spring fishery at the coast of Finnmark. The lack of significant changes for the 3 and 4 year old trawl caught cod may be a result of gear selectivity operating stronger for these age groups. The observed long-term change took place over a period when the



No simultaneous long-term change has been observed for temperature in the Barents Sea. It is therefore reasonable to assume that the increased lengths at age are linked to the overall reduction in stock size.

Growth related to the abundance of capelin

The importance of capelin in the diet of cod has been thoroughly documented for the Northeast Arctic cod (Ponomarenko and Ponomarenko 1975, Ponomarenko and Yaragina 1978, Mehl 1989). Nevertheless, no close correlation was found between estimates of capelin abundance and growth of the cod. As found by Mehl (1989), cod mainly feed on capelin during the capelin spawning season in late winter to early spring. In some years, however, the spawning migration route and the spawning area do not coincide with the distributional area of cod. Thus, although capelin is abundant, it may not always be equally available to the cod. The importance of capelin in the diet of cod has also been documented for cod at Newfoundland/Labrador (Lilly 1987), but no significant correlation was found between capelin abundance and growth of cod (Akenhead et al. 1982).

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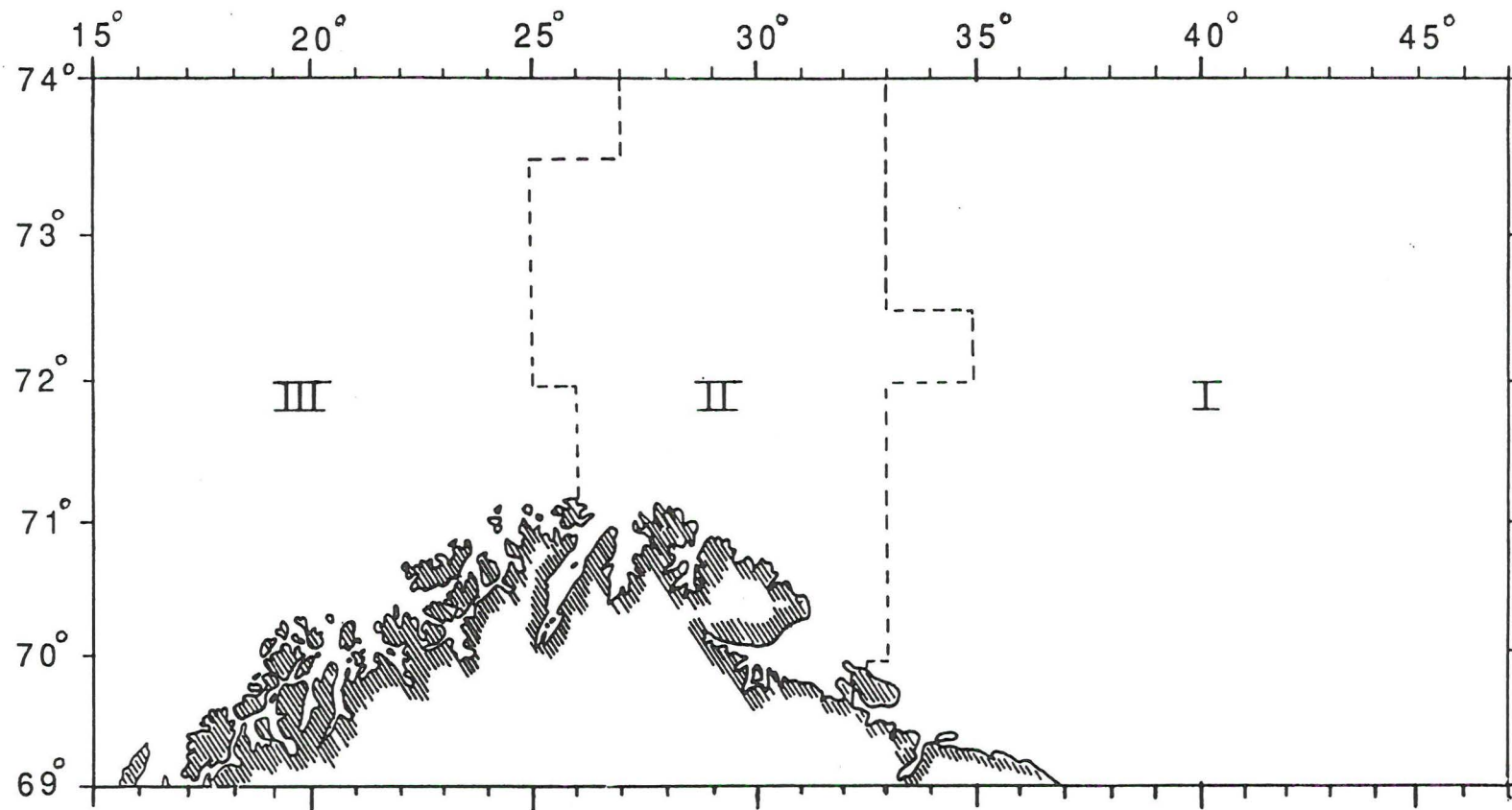
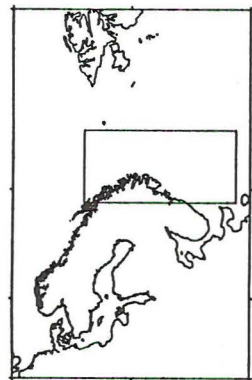


Fig. 1. The study area, with the three subareas used in the analysis of geographical variation in mean length at age.



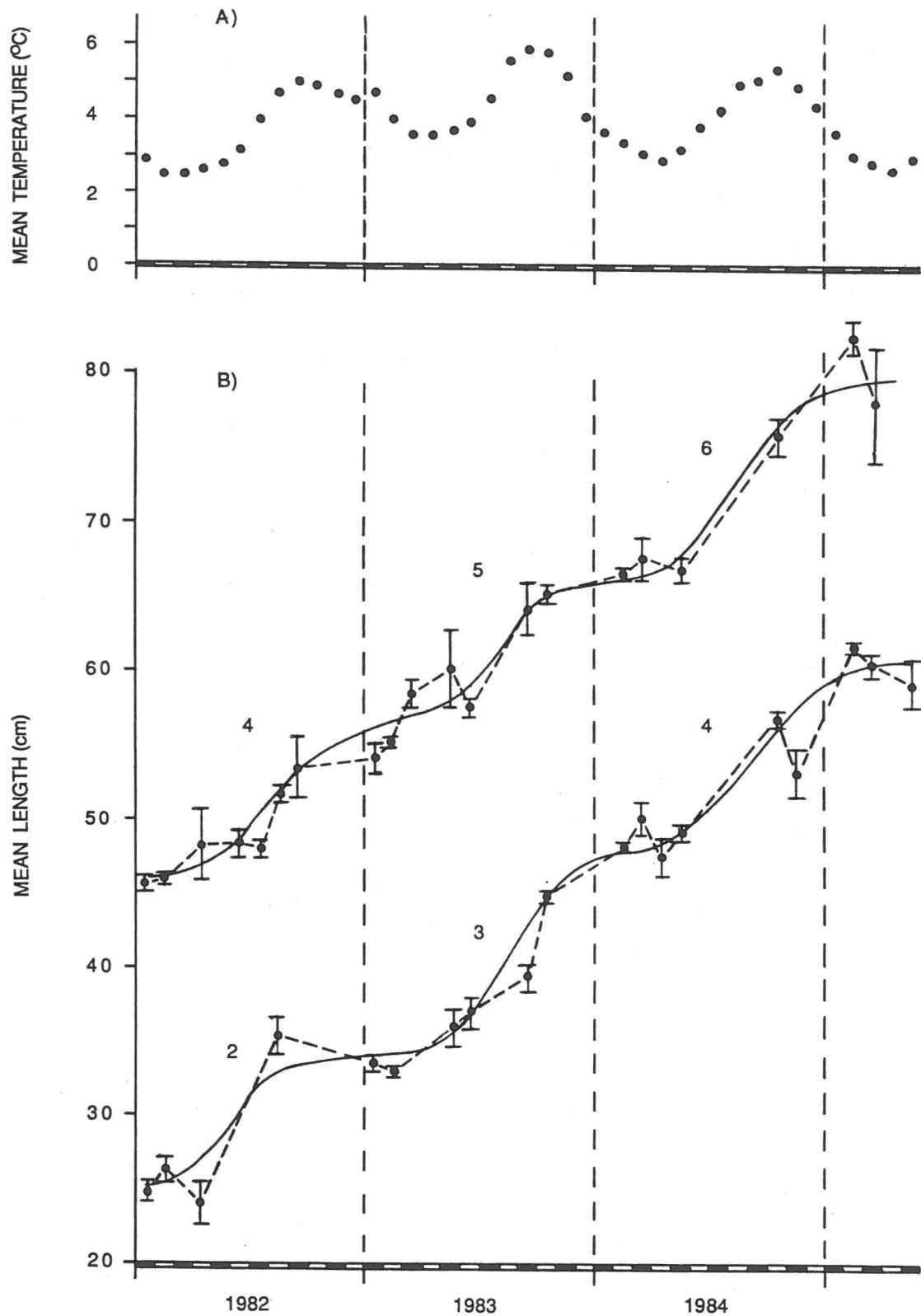


Fig. 2. (A): Monthly mean temperatures in the Kola section in the period January 1982 to May 1985 and (B): monthly mean lengths at age for the year classes 1978 and 1980 during the same period. Standard errors of estimated mean lengths are indicated by the vertical bars. The seasonal growth curves (unbroken line) were fitted by eye.

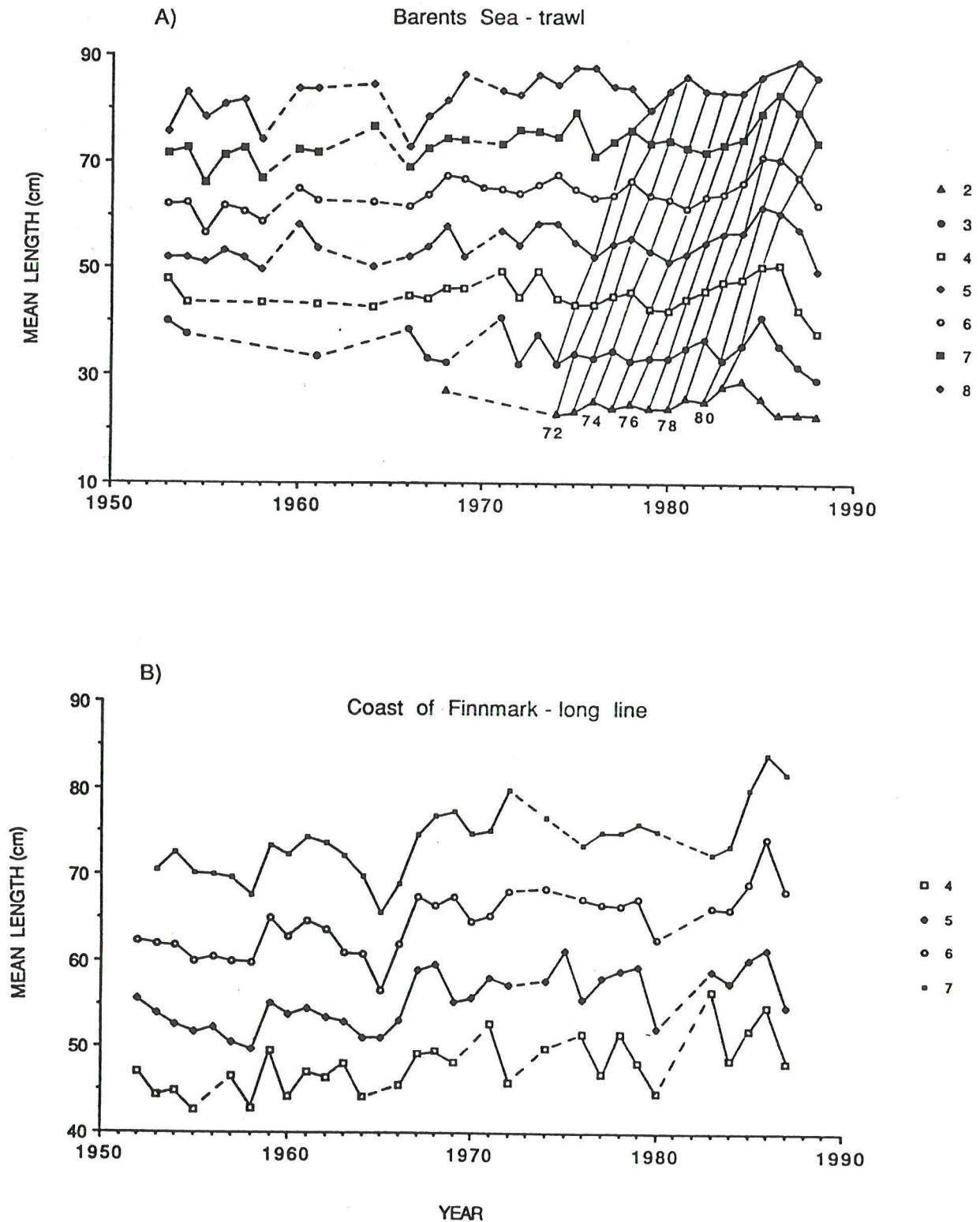


Fig. 3. Long-term variation in mean lengths at age for immature Northeast Arctic cod between 1953 and 1988. All estimated means are based on a minimum of 10 observations. A: Data from Norwegian trawl surveys in the Barents Sea (age groups 2 to 8 years). Growth curves of year classes 1971 to 1981 are also shown. B: Data from the commercial long line fishery in spring off the coast of Finnmark, North Norway (age groups 4 to 7 years).

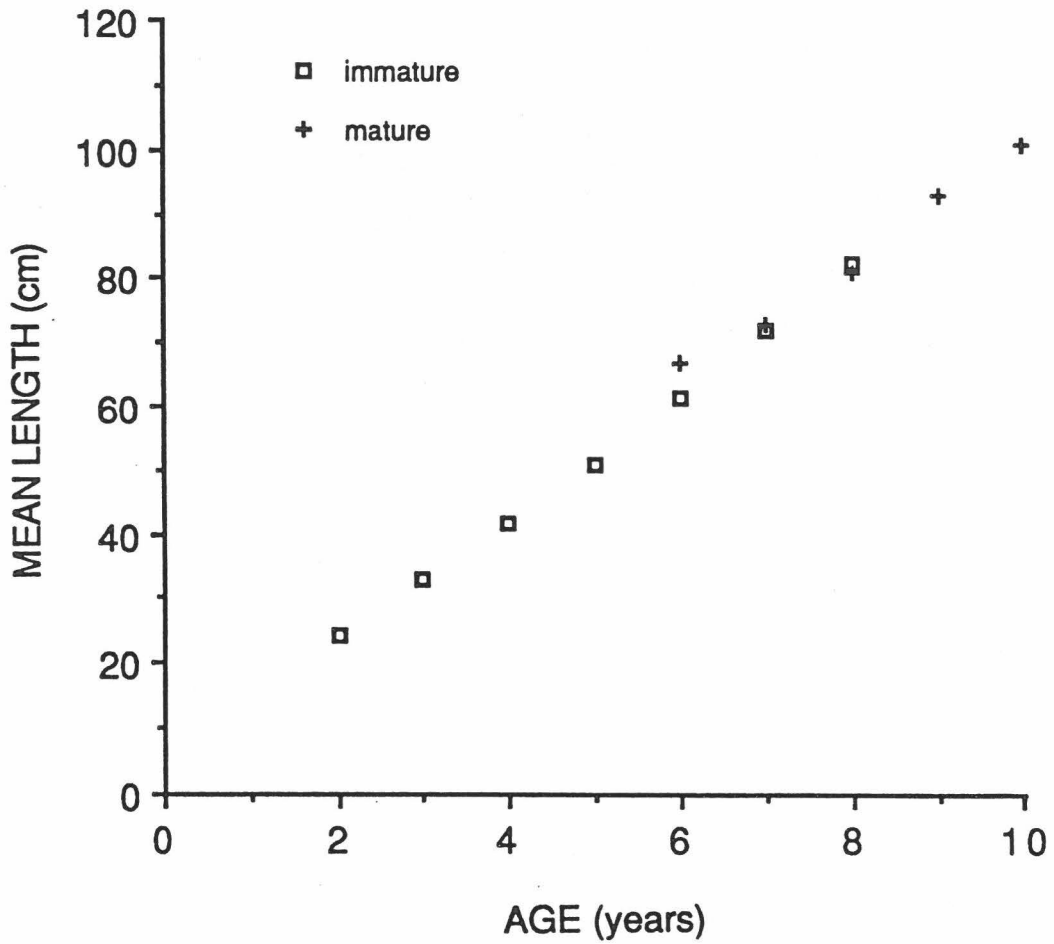


Fig. 4. Mean lengths at age for cod of the 1975 year class within the age range 2 to 10 years. Standard errors of mean lengths were all less than 0.5 cm. The linear growth equation based on these observations were:  $\text{length}(\text{age}) = 9.6 \text{ age} + 5.4$ ;  $n = 12$ ;  $R^2 = 0.98$ . Immature fish were caught by trawl in the Barents Sea, mature fish were caught by long lines at Lofoten.

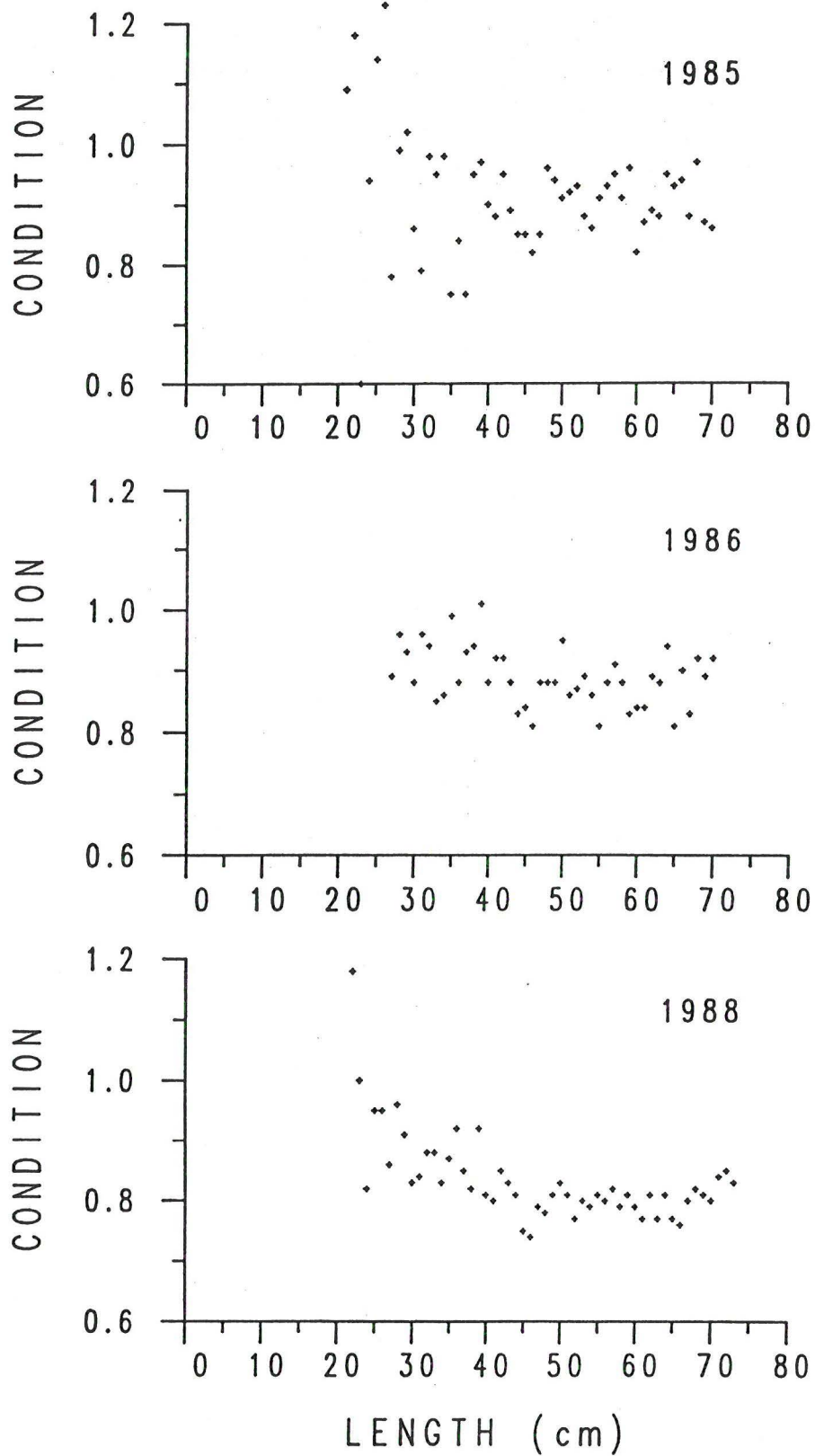


Fig. 5. Median weight at length of Northeast Arctic in 1985, 1986 and 1988 relative to the values in 1984. Computations of median weight at length were made for each 1 cm length interval.

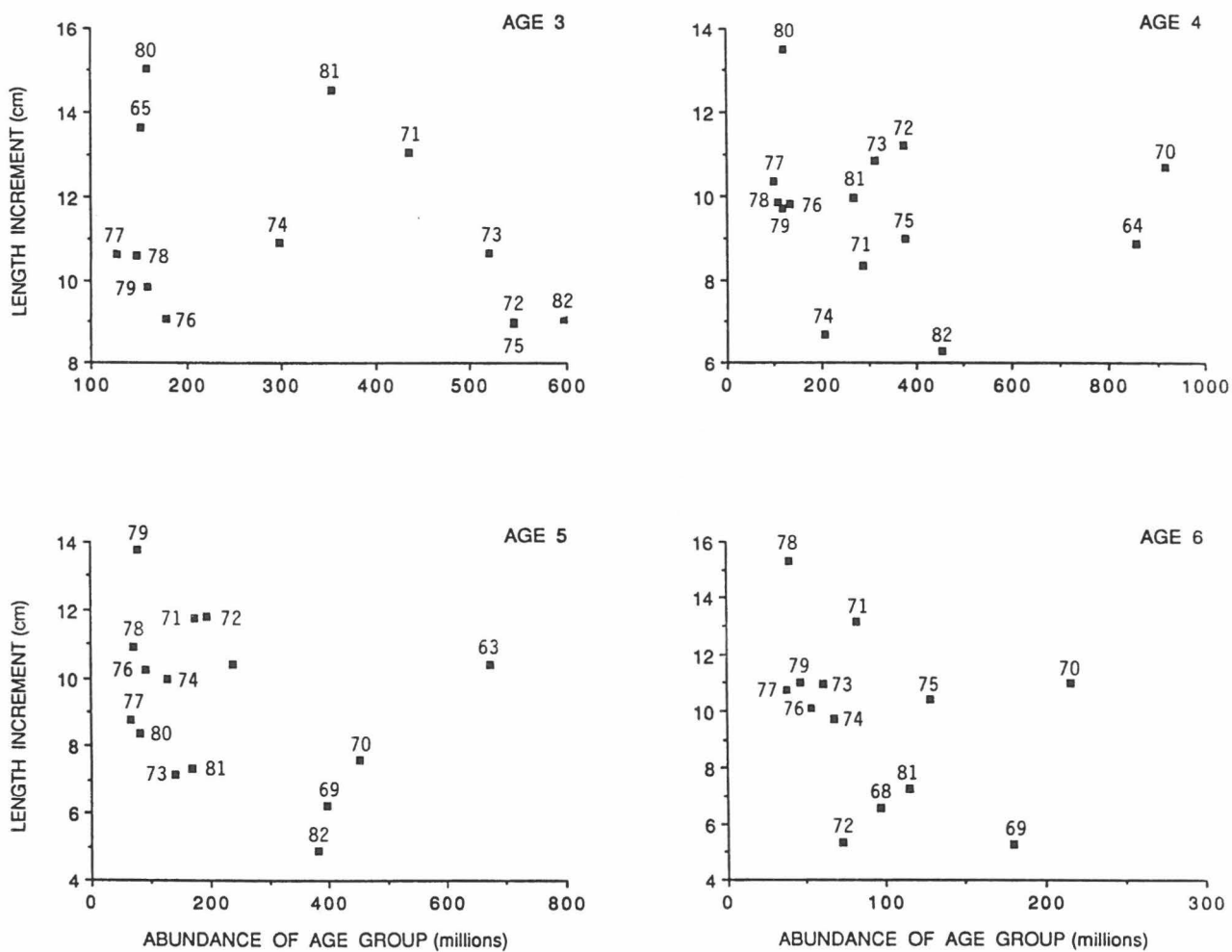


Fig. 6. Annual length increment (growth rate) versus year class abundance for each of the age groups 3 to 6 years. Labels show year classes.

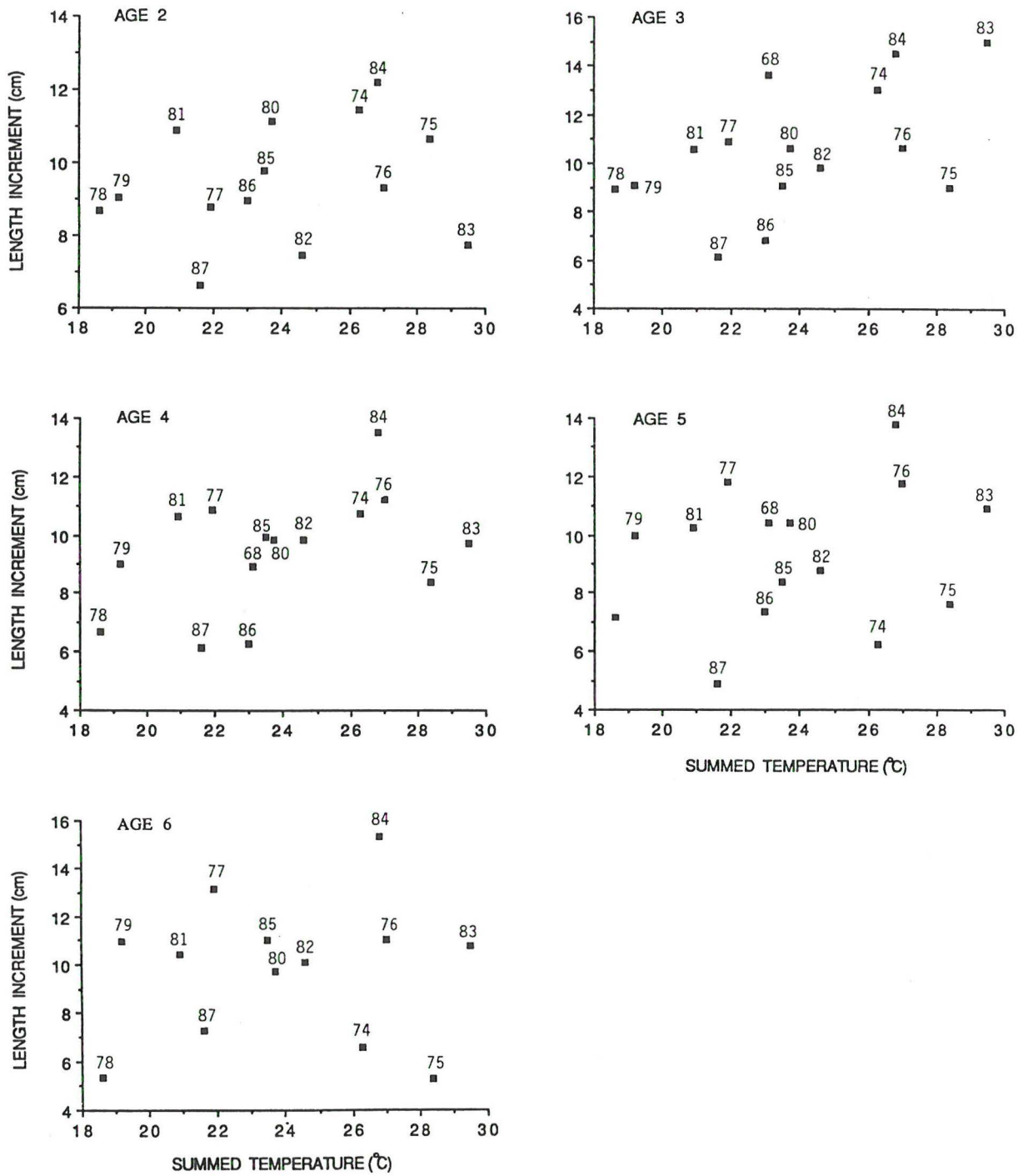


Fig. 7. Annual length increment (growth rate) versus summed temperature in the Kola section from May to October in the corresponding year. Labels show year of sampling.

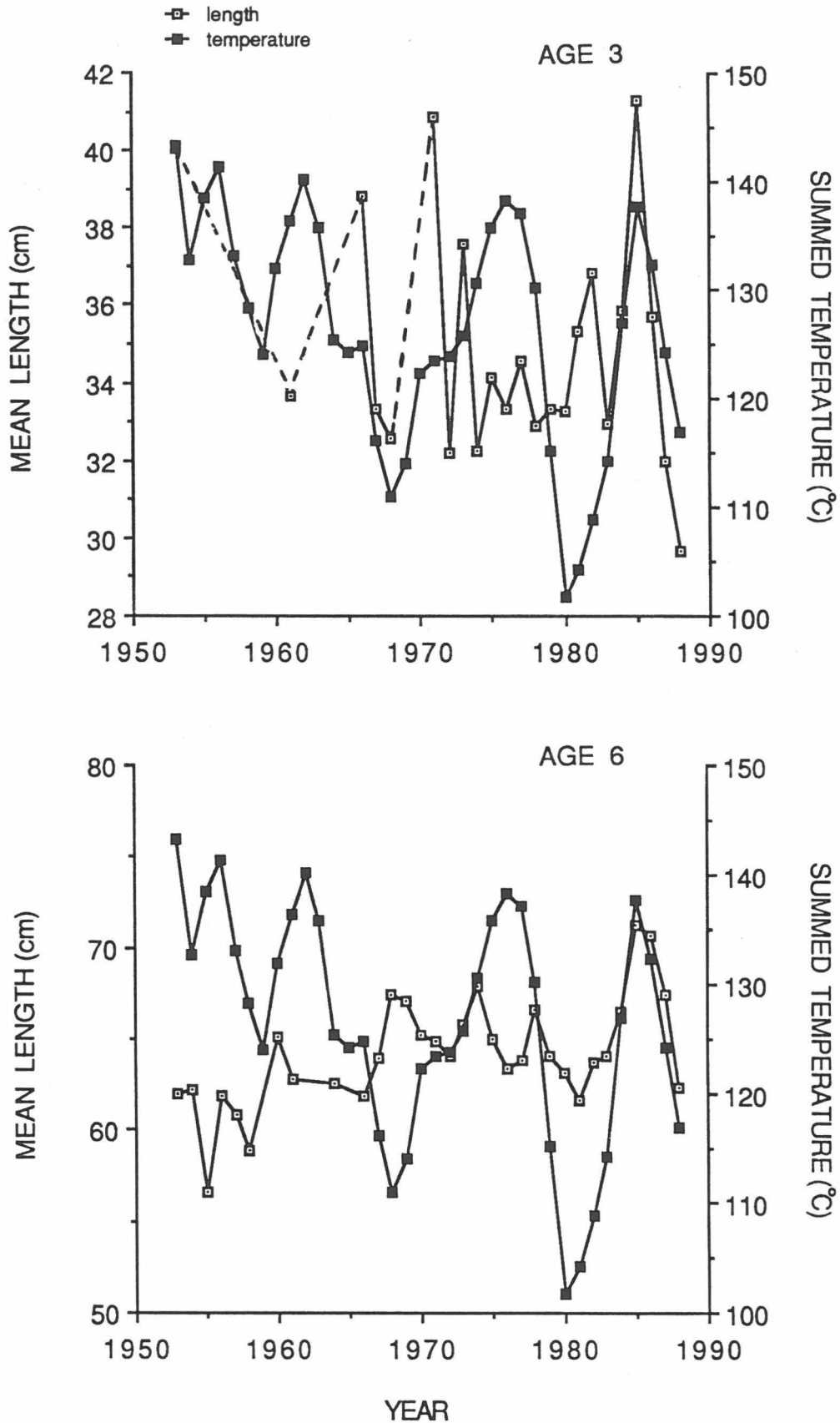


Fig. 8. Fluctuations in mean length at age plotted with corresponding fluctuations in summed monthly mean temperatures in the Kola section across the fish's life (i.e. from May in year when hatched to January in year when caught). Data are given for age groups 3 and 6.

Table 1. Mean length at age in each of the 3 subareas (see Fig. 1) for each year in the period 1983 to 1988. Number of measurements in each subarea in brackets.

Age	Year	Area I	Area II	Area III
2	1983	28.73 ( 26)	27.31 ( 16)	25.00 ( 2)
	1984	27.17 (229)	29.93 (338)	30.81 ( 36)
	1985	23.75 (332)	25.86 (133)	27.46 ( 91)
	1986	20.34 (198)	22.92 ( 39)	25.82 ( 11)
	1987	19.77 (166)	21.57 (249)	23.22 ( 18)
	1988	21.76 ( 42)	22.62 ( 92)	23.50 ( 4)
3	1983	33.49 ( 49)	32.38 ( 45)	33.42 ( 12)
	1984	33.75 ( 40)	36.11 (340)	36.67 ( 64)
	1985	37.42 (106)	41.01 (264)	44.43 (212)
	1986	34.43 (175)	36.25 (218)	36.43 (208)
	1987	30.12 ( 50)	31.82 (215)	33.43 ( 80)
	1988	26.77 ( 22)	29.66 (247)	30.75 ( 36)
4	1983	47.37 ( 32)	45.32 ( 57)	47.38 ( 90)
	1984	47.98 ( 54)	47.88 (192)	48.60 ( 60)
	1985	48.65 ( 84)	49.81 (285)	51.95 (254)
	1986	51.42 ( 95)	49.28 (149)	51.12 (307)
	1987	38.36 ( 28)	41.31 (318)	44.01 (396)
	1988	31.00 ( 1)	37.36 (141)	39.35 ( 62)
5	1983	55.25 ( 8)	54.39 ( 95)	56.46 (171)
	1984	55.26 ( 23)	55.16 (150)	58.23 (119)
	1985	61.25 ( 24)	62.48 (119)	60.56 (106)
	1986	61.17 ( 23)	60.09 (131)	60.57 (327)
	1987	46.00 ( 1)	55.85 ( 41)	57.25 (189)
	1988	45.00 ( 1)	47.19 (280)	49.66 (267)
6	1983	63.00 ( 2)	61.20 ( 46)	64.22 (109)
	1984	67.37 ( 19)	66.60 (109)	66.49 ( 63)
	1985	75.50 ( 8)	71.08 ( 24)	68.60 ( 40)
	1986	71.00 ( 1)	69.85 ( 47)	69.88 ( 64)
	1987	( 0)	69.08 ( 24)	67.20 ( 49)
	1988	( 0)	58.23 ( 39)	62.50 (101)



Table 2. Results of a two-way ANOVA of length at age for age groups 2 to 6 with respect to subarea (see Fig.1) and year of sampling. The analysis was based on data from 1984 to 1987 for the 2 year olds, 1983 to 1988 for the 3 year olds and 1983 to 1987 for the 4 year olds. For the 5 and 6 year olds, the analysis was made for subareas II and III for the years 1983 to 1988.

Age	Source of variation	df	Mean square	F
2	Year (Y)	3	2075.80	170.04 **
	Area (A)	2	1179.97	96.66 **
	Y x A	6	15.56	1.27
	Error	1828	12.21	
3	Year (Y)	5	4584.09	270.19
	Area (A)	2	693.88	40.90
	Y x A	10	155.96	9.19 **
	Error	2365	16.97	
4	Year (Y)	4	3797.09	201.23
	Area (A)	2	686.25	36.37
	Y x A	8	132.92	7.04 **
	Error	2386	18.87	
5	Year (Y)	5	8945.90	415.66
	Area (A)	1	587.84	27.31
	Y x A	5	213.11	9.90 **
	Error	1983	21.52	
6	Year (Y)	5	1552.92	70.26
	Area (A)	1	31.72	1.43
	Y x A	5	164.68	7.45 **
	Error	703	22.10	

\* - significant at 5% level

\*\* - significant at 1% level

Table 3. Summary of a one-way ANOVA of geographical differences in length-at age of age groups 2 to 6. Only years with a minimum of 10 fish in each subarea have been included. For the 5 and 6 year olds a comparison was made for areas II and III only.

Age	Year	Source of variation	df	Mean square	F
2	1984	Area	2	584.76	46.28 **
		Error	600	12.63	
	1985	Area	2	578.48	37.12 **
		Error	553	15.58	
	1986	Area	2	242.47	21.85 **
		Error	245	11.10	
	1987	Area	2	209.73	26.54 **
		Error	430	7.90	
3	1983	Area	2	15.62	1.21
		Error	103	12.95	
	1984	Area	2	117.86	9.87 **
		Error	441	11.95	
	1985	Area	2	1821.08	78.40 **
		Error	579	23.23	
	1986	Area	2	226.60	10.18 **
		Error	598	22.25	
	1987	Area	2	172.60	15.37 **
		Error	342	11.23	
	1988	Area	2	112.04	11.56 **
		Error	302	9.69	
4	1983	Area	2	82.53	3.38 *
		Error	176	24.40	
	1984	Area	2	11.95	0.92
		Error	303	13.11	
	1985	Area	2	478.53	28.76 **
		Error	620	16.64	
	1986	Area	2	201.94	11.12 **
		Error	548	18.16	
1987	Area	2	906.49	40.63 **	
	Error	739	22.31		
5	1983	Area	1	260.84	15.51**
		Error	264	16.81	
	1984	Area	1	624.14	27.10 **
		Error	267	23.03	
	1985	Area	1	207.18	10.91 **
		Error	223	18.99	
	1986	Area	1	21.02	1.85
		Error	456	11.36	
1987	Area	1	65.56	2.28	
	Error	228	28.78		
1988	Area	1	833.63	28.20 **	
	Error	545	29.56		
6	1983	Area	1	295.92	14.76 **
		Error	153	20.05	
	1984	Area	1	0.43	0.02
		Error	170	19.40	
	1985	Area	1	92.50	2.75
		Error	62	15.84	
	1986	Area	1	0.02	<0.01
		Error	109	16.93	
1987	Area	1	56.89	3.63	
	Error	71	15.66		
1988	Area	1	514.00	17.18 **	
	Error	138	29.91		

\* - significant at 5% level

\*\* - significant at 1% level

Table 4. Results of a two-way ANOVA of length-at-age with respect to sex and year for age groups 2 to 7 based on data for the period 1974 to 1988.

Age	Source of variation	df	Mean square	F
2	Year (Y)	14	929.36	86.06 **
	Sex (S)	1	34.13	3.16
	Y x S	14	11.69	1.08
	Error	2365	10.80	
3	Year (Y)	14	3190.92	148.64 **
	Sex (S)	1	0.68	0.03
	Y x S	14	20.08	0.94
	Error	4605	21.47	
4	Year (Y)	14	5016.20	214.40 **
	Sex (S)	1	0.04	< 0.01
	Y x S	14	26.07	1.11
	Error	6698	23.40	
5	Year (Y)	14	5847.78	88.70 **
	Sex (S)	1	9.46	0.14
	Y x S	14	65.93	2.34
	Error	7449	28.14	
6	Year (Y)	14	1273.61	45.59 **
	Sex (S)	1	419.62	15.02 **
	Y x S	14	23.04	0.82
	Error	2678	27.93	
7	Year (Y)	14	394.53	12.70 **
	Sex (S)	1	123.66	3.98 *
	Y x S	14	35.42	1.14
	Error	819	31.06	

\* - significant at 5% level

\*\* - significant at 1% level

Table 5. Mean length-at-age and numbers in samples of mature and immature cod of age groups 5 to 7 for each year in the period 1970 to 1988. Only years with observations have been included. For years with 10 or more observations in each group, the difference in mean length between mature and immature has been computed. Years for which significant differences were observed have been indicated.

Age	Year	Immature	Mature	$\Delta L$
5	1970	49.00 ( 2)	( 0)	
	1971	57.25 ( 12)	62.00 ( 1)	
	1974	56.14 ( 94)	65.00 ( 2)	
	1975	53.80 ( 692)	60.86 ( 7)	
	1976	51.36 ( 122)	61.50 ( 4)	
	1977	54.69 ( 345)	61.09 ( 11)	6.40 **
	1978	55.73 ( 298)	52.67 ( 3)	
	1979	52.34 ( 106)	54.20 ( 5)	
	1980	50.86 (2456)	56.40 ( 83)	5.54 **
	1981	52.40 ( 790)	54.79 ( 43)	2.39 **
	1982	54.55 ( 393)	54.82 ( 11)	0.27
	1983	55.70 ( 274)	55.77 ( 13)	0.07
	1984	56.42 ( 292)	58.51 ( 45)	2.09 *
	1985	61.54 ( 249)	62.95 ( 62)	1.41 *
1986	60.48 ( 482)	60.44 (111)	-0.04	
1987	56.95 ( 231)	59.18 ( 45)	2.23 *	
1988	48.79 ( 656)	51.60 ( 47)	2.81 **	
6	1970	65.14 ( 7)	65.67 ( 3)	
	1971	62.60 ( 5)	68.00 ( 1)	
	1974	66.66 ( 71)	68.60 ( 5)	
	1975	62.39 ( 117)	66.70 ( 10)	4.31 *
	1976	61.40 ( 87)	66.70 ( 4)	
	1977	63.14 ( 146)	68.78 ( 32)	5.64 **
	1978	66.51 ( 88)	69.00 ( 4)	
	1979	62.88 ( 60)	66.25 ( 24)	3.37 *
	1980	62.30 ( 211)	65.79 ( 33)	3.49 **
	1981	61.31 ( 852)	63.76 (125)	2.45 **
	1982	62.63 ( 306)	64.08 ( 93)	1.45 *
	1983	63.32 ( 157)	65.39 ( 28)	2.07 *
	1984	66.64 ( 191)	65.59 ( 63)	-1.05
	1985	70.19 ( 72)	72.60 ( 78)	2.41 **
1986	69.91 ( 113)	71.45 ( 42)	1.54 *	
1987	67.82 ( 73)	67.51 ( 37)	-0.31	
1988	61.84 ( 164)	63.02 ( 54)	1.18	
7	1970	71.25 ( 4)	76.00 ( 3)	
	1971	73.94 ( 18)	76.60 ( 5)	
	1974	73.00 ( 9)	80.50 ( 4)	
	1975	73.25 ( 12)	82.50 ( 6)	
	1976	67.70 ( 10)	72.33 ( 3)	
	1977	72.43 ( 86)	76.10 ( 80)	3.67 **
	1978	76.29 ( 21)	76.00 ( 2)	
	1979	71.83 ( 12)	76.36 ( 11)	4.53
	1980	73.82 ( 62)	73.64 ( 28)	-0.18
	1981	72.03 ( 100)	73.42 ( 45)	1.39
	1982	71.76 ( 338)	72.47 (174)	0.71
	1983	72.76 ( 41)	75.03 ( 36)	2.27 *
	1984	74.05 ( 63)	75.62 ( 26)	1.57
	1985	81.96 ( 23)	82.13 ( 32)	0.17
1986	81.19 ( 26)	84.38 ( 13)	3.19	
1987	83.67 ( 9)	79.38 ( 8)		
1988	75.08 ( 37)	73.38 ( 21)	-1.70	

\* - significant at 5% level

\*\* - significant at 1% level

Table 6. Results of a two-way ANOVA of length at age with respect to stage of maturity (mature, immature) and year for age groups 5 to 7. For the 5 and 6 year olds, the analysis was based on data from 1980 to 1988 and for the 7 year olds data from 1980 to 1986 and for 1988 were used.

Age	Source of variation	df	Mean square	F
5	Year (Y)	8	2979.00	110.45
	Stage (S)	1	884.97	32.81
	Y x S	8	186.33	6.91 **
	Error		26.97	
6	Year (Y)	8	1957.07	73.79
	Stage (S)	1	709.95	26.77
	Y x S	8	80.02	3.02 **
	Error	2674	26.52	
7	Year (Y)	8	1138.98	36.31 **
	Stage (S)	1	118.58	< 3.78
	Y x S	8	31.58	1.01
	Error	1049	31.37	

\* - significant at 5% level

\*\* - significant at 1% level

Table 7. Trends in mean length-at-age of cod across the period 1953 to 1988. N = number of year's data used; r = linear correlation coefficient; b = regression coefficient (cm/year); change = estimated increase in mean length at age between 1953 and 1988.

Trawl - Barents Sea				
Age group	N	r	b	change
3	23	0.278	-0.097	-
4	27	0.058	0.017	-
5	30	0.410 *	0.121	4.2
6	33	0.625 **	0.207	7.3
7	31	0.611 **	0.196	6.9
8	26	0.490 *	0.145	5.1
Long line - Finnmark				
Age group	N	r	b	change
4	29	0.640 **	0.200	7.0
5	33	0.721 **	0.221	7.7
6	32	0.728 **	0.252	8.8
7	31	0.686 **	0.270	9.5

\* - significant at 5% level

\*\* - Significant at 1% level

Table 8. Trends in mean length-at-age of cod across the period 1968 to 1988. N = number of year's data used; r = linear correlation coefficient; b = regression coefficient (cm/year).

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Trawl - Barents Sea			
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Age group	N	r	b
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2	14	0.095	-0.035
3	15	0.114	-0.074
4	16	0.040	0.022
5	16	0.183	0.099
6	16	0.252	0.142
7	14	0.490	0.390
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Table 9. Growth rate (length increment in cm) of age groups 2 to 6 for the years 1974 to 1988.

Year	age group				
	2	3	4	5	6
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1974	11.46	13.07	10.72	6.25	6.59
1975	10.69	9.01	8.37	7.60	5.31
1976	9.32	10.69	11.22	11.78	11.03
1977	8.78	10.92	10.86	11.82	13.15
1978	8.69	8.95	6.69	7.15	5.32
1979	9.03	9.08	9.01	9.96	10.94
1980	11.14	10.66	9.83	10.45	9.73
1981	10.91	10.59	10.64	10.23	10.45
1982	7.48	9.84	9.86	8.77	10.13
1983	7.76	15.03	9.70	10.94	10.73
1984	12.22	14.55	13.50	13.77	15.32
1985	9.79	9.08	9.95	8.37	11.00
1986	8.98	6.86	6.27	7.34	-
1987	6.66	6.14	6.15	4.89	7.26
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Table 10. The Spearman rank correlation coefficients for the comparison of growth of different age groups in the same year. Computations based on the values of Table 6. Significance levels from Table P in Siegel (1956) with  $n=14$ .

Age group	2	3	4	5	6
2	1.00				
3	0.23	1.00			
4	0.39	0.79 **	1.00		
5	0.11	0.71 **	0.69 **	1.00	
6	0.07	0.53 *	0.70 **	0.81 **	1.00

\* - significant at 5% level

\*\* - significant at 1% level

Table 11. Estimated parameters for the length-weight relationship calculated separately for the years 1984 to 1986 and 1988.  $a$  and  $b$  are the parameters of the length-weight relationship ( $W = aL^b$ ) and  $n$  is the number of observations.

Year	$n$	$a(x10^{-3})$	$b$	$r^2$	95% conf. interval. for $b$
1984	1190	5.15	3.15	0.99	3.13, 3.17
1985	820	5.36	3.11	0.94	3.04, 3.18
1986	582	8.18	3.00	0.98	2.96, 3.04
1988	1372	9.20	2.95	0.99	2.93, 2.98

Table 12. Correlation coefficients between growth increment and average annual abundance estimates for the same year.  $N_I$  = abundance of the year class;  $N_{II}$  = abundance of the year class plus that of the preceding and following year classes (for age 3 only the following);  $N_{III}$  = the abundance of cod three years and older;  $n$  = number of year's data used.

period	age	$n$	$N_I$	$N_{II}$	$N_{III}$
1968-1987	3	13	-0.344	0.162	0.069
	4	14	-0.142	-0.090	-0.079
	5	15	-0.314	-0.196	-0.131
	6	13	-0.348	-0.591 *	-0.435
	7	5	0.045	0.380	0.079
1953-1987	4	21	-0.186	-0.163	-0.202
	5	26	-0.111	-0.124	0.012
	6	27	-0.218	-0.189	-0.122
	7	22	0.179	0.145	0.076

\* - significant at 5% level

Table 13. Correlation coefficients between annual growth increment and temperature indices (summed monthly means in the Kola section for the whole calendar year and for the growth season (e.g. May to October)). n is the number of observation pairs.

age	n	$\Sigma T_{\text{January-December}}$	$\Sigma T_{\text{May-October}}$
2	14	0.184	0.234
3	15	0.490	0.525 *
4	15	0.353	0.423
5	15	0.209	0.241
6	13	0.079	0.102

\* - significant at 5% level

Table 14. Correlation coefficients between length at age and summed temperature indices across the life span of an age group (i.e. from hatching to time when caught). The temperature indices refer to monthly mean values in the Kola section and n is the number of years with observation pairs for each age group in the period 1953 to 1988.

age	n	Life-span temperature
3	23	0.298
4	27	-0.058
5	30	-0.248
6	32	-0.445 **
7	31	-0.475 **

\*\* - significant at 1% level

Table 15. Correlation coefficients between growth rate of cod and spawning stock estimates of capelin. n refers to number of observation pairs. Spawning stock biomass estimates of capelin were taken from Anon. (1988).

age	n	$SSB_{\text{Capelin}}$
3	14	0.102
4	14	0.338
5	14	0.365
6	13	0.193



APPENDIX I.

Stock size of Northeast Arctic cod for the years 1953 to 1964 estimated by VPA. Catch at age data were taken from the ICES data base and the starting F values for the iteration were taken from Anon. (1988). Estimates are given for age groups 3 to 15 (15 is a plus group) and refer to 1 January each year. All numbers are in thousands.

YEAR	AGE												
	3	4	5	6	7	8	9	10	11	12	13	14	15+
1953	1592638	954402	602567	228712	89559	62697	34030	28617	12702	4392	1305	419	378
1954	644166	1261144	684358	392516	137377	52892	36187	18389	13978	5363	2028	649	298
1955	273054	517041	892709	428650	230851	76006	33668	19054	7415	5420	2273	860	310
1956	440309	220034	389353	549428	206483	113732	34981	15297	7145	2388	2288	1085	402
1957	805081	350912	158361	202400	226124	91450	47473	15242	5864	2333	493	724	419
1958	497214	643506	256710	105185	102352	107222	39817	22975	6916	1925	823	97	341
1959	684953	378919	406714	146379	49652	49430	55702	20642	9455	2727	624	448	273
1960	791122	531631	240124	200165	71941	24086	24581	24929	8431	4387	1339	284	629
1961	919153	613522	347189	138918	103438	38168	12166	13627	9987	2892	1943	779	300
1962	731056	711499	383013	173640	67909	49997	15729	4792	5112	3230	873	779	286
1963	473645	560265	429237	164112	62437	30293	21278	5785	1498	1865	1176	364	444

