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AMBIENT TEMPERATURE AND DISTRIBUTION OF NORTHEAST ARCTIC COD

by

Geir Ottersen, Kathrine Michalsen and Odd Nakken.

Institute of Marine Research, Bergen

P. O Box 1870, N-5024 Bergen, Norway

ABSTRACT

Most studies on the effects of field temperature on fish distribution and population parameters have considered the temperature and its variability at fixed stations or sections rather than the temperature in the actual surroundings of the fish, the ambient temperature. From spatial distribution of fish density and temperature, estimates of ambient winter temperature were established for 1-7 year old Northeast arctic cod in the period 1988-1995. Four different estimates were calculated for each age and year based on fish density observations from acoustic- and bottom trawl surveys and temperature recordings in two depth layers, bottom as well as 100m depth-bottom. The estimates of ambient temperature were compared and also examined in relation to temperature series in fixed areas and a standard section, the Kola meridian. As expected the interannual variability in ambient winter temperature was found to be larger than in the Kola-section series. The ambient temperatures were found to increase with age. For the younger age groups the ambient temperature seemed to decrease with increasing numbers of fish. The mean ambient temperatures are also compared with the temperatures used for calculations of growth and consumption rate in cod in the ICES Working groups.

INTRODUCTION

Most workers studying the effects of field temperatures on fish distribution and population parameters have considered the temperature and its variations at fixed locations rather than the temperature actually surrounding the fish, the ambient temperature. Since fish often inhabit regions of relatively large horizontal gradients they may, depending on their migrations, experience temperature variations which are quite different from those in any geographically fixed point.

Within the area of distribution of Northeast arctic cod, the Barents Sea and Svalbard waters (Figure 1), annual mean temperatures range from 6-8 °C at the spawning grounds along the west coast of Norway (Aure and Østensen, 1993) down to 0 °C or even -1 °C along the Polar front in the northern and north-eastern parts where the fish feed during summer and Autumn (Mehl *et al.*, 1985; Woodhead and Woodhead, 1965). Cod is mainly found at depths below 100 metres (Korsbrekke *et al.* 1995) where seasonal variations at a fixed locations are rather small, 1-3 °C (Ottersen and Ådlandsvik, 1993). Consequently the majority of adult specimens, more than 7 years of age, experience significantly higher temperatures during their migrations to and from the spawning grounds in November- May than during summer-autumn when feeding. A similar seasonal migration, though less in extent, takes place for the immature fish, ages 3-6 years, which prey on capelin migrating towards the coasts of Russia and Northern Norway in winter/spring (Mehl *et al.* 1985). Seasonal migrations of the younger fish, age 1 and 2 years, appear to be smaller. Particularly the 1 year old cod seem to remain in the areas where they settled during autumn as 0-group, at the end of their pelagic drift phase (Baranenkova, 1957; Maslov, 1944 and 1960). In accordance with these seasonal movements through the temperature field one would expect that ambient temperatures of the various agegroups of Northeast arctic cod as a rule are higher during winter-spring than summer-autumn. One would also expect that ambient winter temperatures increase by age as demonstrated by Nakken and Raknes (1987) and Shevelev *et al.* (1987).

In addition to these seasonal variations, temperature related displacement has been reported on the interannual time scale as well as on both small and large spatial scales (see Nakken and Raknes, 1987 for references). In periods of warm climate the cod distribution area is extended towards the east and north as compared to periods of cold climate when the fish tend to concentrate in the southwestern part of the Barents Sea. Positive effects of higher temperatures on recruitment and growth have also been shown (see

Ottersen *et al.*, 1994; Nakken, 1994, and Ottersen and Sundby, 1995 for references), and increased mortality of fingerlings due to food limitation at low temperatures has been suggested in numerous Russian works (see Ponomarenko, 1984 for references).

In the annual stock assessment of Barents Sea cod and capelin sea temperatures are now being used quantitatively both in estimating the cods annual consumption of prey species, particularly capelin, and in predicting cod growth (Anon. 1996a; Anon. 1996b). In lack of estimates of actual ambient temperatures, climatological temperatures (Ottersen and Ådlandsvik, 1993) in some few fixed points are used together with temperatures from the Kola section (Bochkov, 1982) which capture the temporal variability (Bogstad and Mehl, in prep.).

Brander (1995) who examined 17 North Atlantic cod stocks including Northeast arctic found that most of the observed variability in growth was due to temperature. The main conclusion he drew from his study was: "More attention should be paid to quantifying the effect of temperature on growth of cod (and perhaps other species), because it probably has significant effects on stock assessment, catch forecasting, and evaluation of the consequences of climate change. In order to investigate the effect in detail for individual stocks, data on temperature and fish distribution need to be analysed jointly".

The present work describes alternative methods of estimating the ambient temperature of each agegroup of Northeast arctic cod, and the differences in results obtained by the various methods are analysed and discussed. Variability in ambient temperature between different agegroups and years are studied. We have also assessed the changes the use of our results would generate in the estimates of consumption arrived at by the ICES Atlanto-Scandian Herring, Capelin and Blue Whiting Assessment Working Group (Bogstad and Mehl, in prep.).

MATERIAL AND METHODS

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 ABCD (Figure 2), while the acoustic registrations covered a slightly larger area. The number of trawl stations have been between 230 (1989) and 383 (1995). Since 1993 the two areas have been the same and expanded to the north and east in order to cover the geographical distribution of the younger age groups of cod satisfactory. Abundance estimates, numbers at age, acoustic and swept area, for all years are available in Anon. (1996a). 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).

Monthly 0-200m depth sea temperature averages from the Russian hydrographical section off the Kola Peninsula (Bochkov, 1982) are used. The position of the part of the Kola section used is shown in Figure 2.

The annual temperature of the water masses actually surrounding the fish, the ambient temperature, was defined as density weighted temperature means for each age-group and estimated by the following equation:

$$\overline{T_{amb}^{annual}} = \frac{\int \rho(x, y, z, t) \cdot T(x, y, z, t)\, dxdydzdt}{\int \rho(x, y, z, t)\, dxdydzdt} \qquad (1)$$

where $\rho(x, y, z, t)$ is fish density at position (x, y, z) and time t, $T(x, y, z, t)$ the corresponding temperature, and the integration is done over the whole distribution volume of the fish and the year. In our case t is fixed to February reducing equation (1) to

$$\overline{T_{amb}} = \frac{\int \rho(x, y, z) \cdot T(x, y, z)\, dxdydz}{\int \rho(x, y, z)\, dxdydz} \qquad (2)$$

The ambient temperature calculated for this time is taken to be representative of the temperature conditions the cod have lived in throughout the winter. Equation (2) was used to compute four estimates of ambient temperature for each age and year. Each of the two types of density estimates (acoustic and swept area) were combined with the temperature at the bottom and the average temperature in the 100m depth to bottom layer. Procedures of data processing and analyses are given in the following.

Temperature

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 (or surface) to the bottom was taken to represent the temperature of the total vertical range inhabited by the cod. These temperature values were then interpolated horizontally to a (nearly) equidistant polarstereographic grid of 68 times 61 cells each of 20 times 20 km. A combination of Laplace and spline interpolation was used, the Laplace-spline equation solved iteratively by the method of successive over-relaxation (SOR, e. g. Smith, 1985 or Haltiner and Williams, 1980). The interpolation scheme is explained by Taylor (1976) while the actual programs used are described by Ottersen (1991).

Temperature values representative for each 30 minutes latitude times 1 degree longitude acoustical rectangle were calculated by averaging the values from the smaller polarstereographic grid cells within the rectangle. Mean temperatures within each subarea (Figure 2), within the ABCD area, and for the whole area covered were calculated by taking the arithmetic mean of values belonging to the rectangles within the area in question.

Swept area densities

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.

$$\rho = c / (d\ s) \qquad (3)$$

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 3 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 the different standard areas (Figure 2). 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.

Acoustic densities

The acoustic method and computation procedures used are described in several textbooks (Gunderson, 1993; MacLennan and Simmonds, 1991; Fernø and Olsen, 1994), and for these particular surveys in Dalen and Nakken (1983), and Korsbrekke *et al.* (1995). Density estimates (number of fish per unit area, ρ) were calculated for each 5 cm length group.

$$\rho = (s_A/\bar{\sigma}) . p \qquad (4)$$

where s_A is acoustic backscattering per unit area for cod

$\bar{\sigma}$ is the mean scattering cross section of individual fish

p is the proportion of fish in the length group from swept area estimates

Equation (4) is applied for rectangles of 30 minutes latitude and 1 degree longitude, from surface to the bottom, using mean values of s_A, $\bar{\sigma}$ and p as input. Estimated density at length is converted to absolute numbers at length by multiplying with the area of the rectangle. As for the swept area estimates, numbers at length are converted to numbers at age by applying age/length keys.

Mass centre of distribution

The centres of mass of the fish distributions were calculated separately for each age group and year based on the acoustic estimates described immediately above. The longitudinal and latitudinal coordinates of the centres of mass of distribution are averages of the coordinates of each acoustical square weighted by the number of fish, N (x, y), estimated in the square,

$$\overline{lon} = \sum (N(x,y) \cdot lon(x,y)) / \sum N(x,y), \text{ and} \qquad (5)$$

$$\overline{lat} = \sum (N(x,y) \cdot lat(x,y)) / \sum N(x,y)$$

Ambient temperature estimates

Ambient temperature values based on acoustic density estimates were worked out by means of the temperature values calculated above representative for the same acoustic rectangles. Mean ambient temperatures were determined separately for each agegroup and year from Equation (2), in practice by dividing the sum over all rectangles of the products of number of fish and temperature with the sum of numbers of fish:

$$\overline{T_{amb}} = \sum (N(x,y) \cdot T(x,y)) / \sum N(x,y) \qquad (6)$$

Relative frequency distributions within temperature intervals were calculated separately for each agegroup and year by summing the number fish in acoustical rectangles with temperatures within the interval in question and dividing by the total number of fish. Swept area estimates and temperatures were combined using Equation (2) in the following manner. Each trawl station was first given the temperature value of the polarstereographic cell in which it is situated. Mean ambient temperatures for each agegroup and year were then worked out as

$$\overline{T_{amb}} = \left(\sum_{int<-1}^{int\geq 7} N_{int} \cdot T_{int} \right) \Big/ \sum_{int<-1}^{int\geq 7} N_{int} \qquad (7)$$

where $N_{int} = Area_{int} \cdot \rho_{int}$, i.e. the total number of fish in each temperature interval is estimated as the area covered by such watermasses multiplied by the average density of fish caught within this temperature interval. The temperature intervals range from below -1 °C to above or equal to 7 °C in steps of half a degree giving a total of 18 intervals, t_{int} is the midpoint in each interval ranging from -1.25 °C to 7.25 °C. Relative frequency distributions within temperature interval int were in this case worked out for each agegroup and year as $N_{int}/\sum N_i$.

Linear regression analyses between different ambient and mean temperatures, with and without allowing for an intercept, were performed separately for each agegroup by means of the SAS package (SAS Institute, 1988). The choice of regression does not imply belief in any causal relationships, only that the slope and intercept parameters are of interest. The root mean squared error is defined as

$$RMSE = \sqrt{\frac{1}{n-p} \sum_{i=1}^{n} \left(\hat{Y}_i - Y_i \right)^2} \qquad (8)$$

where Y_i are the observed values, $\hat{Y}_i$ the estimates, n the number of observations and p the number of parameters. Linear regression assumes uncorrelated error terms. The Durbin-Watson statistic (SAS Institute, 1992) was used to test for lag 1 autocorrelations which in most cases were found to be not statistically significant at the 5% level.

Paired t-tests (SAS Institute, 1988) were also used to compare the different ambient and mean temperatures separately for each agegroup. While an ordinary t-test would have tested for differences in temporally averaged ambient temperatures, the paired test examines if the difference within single years on average is different from zero. The significance levels should be regarded as approximate, due to the assumptions of normality and independence not being fulfilled for all cases.

RESULTS AND DISCUSSION

Temperature and its variation in space and time

For an extensive description of Barents Sea oceanography several papers by Midttun may be recommended, e.g. Midttun (1989) and Midttun (1990). The general development of winter bottom temperature during the 1988-1995 period is shown in Figure 3 for the subareas given in Figure 2 as well as aggregated within ABCD. More details are shown in Table 1 where temperature means and standard deviations are given both for the bottom and 100m to bottom depth levels as well as the means of the differences in temperature between the levels. The spatial differences in mean temperature between the areas are clearly larger than the temporal variability from year to year. The A, B, C and D areas, covered by survey each year, always have the same order of increasing temperature: D, A, C, B, with the difference between B and D varying from 2.60 °C in 1990 to 3.61 °C in 1991. The dominating interannual temperature variability would seem to be of large scale origin, in syncrony throughout the different areas. The Kola section temperature, which has been used as an indicator of the general Barents Sea temperature situation by several authors, e.g. Borisov and Elizarov (1989) and Ottersen and Sundby (1995), is seen to vary in reasonable accordance with the ABCD temperature mean. The level of temperature in the section is in best accordance with that in subarea A, not with D where it is situated.

As seen by the temperature differences in Table 1 the 100m to bottom temperature is for most areas and years clearly higher than the bottom temperature. There are however systematic dissimilarities between the areas, with the vertical gradient being largest in F and A, while in area B the temperature was actually slightly higher at the bottom for every year from 1990-1995. This can be explained by the convection process connected to the winter cooling of the ocean by the atmosphere not reaching the bottom layer in this area. The standard deviation of temperature differs clearly from subarea to subarea. Typically the smaller areas of B and C have the most homogenous water masses. In some years the variability in the large D', E and F areas is small, but this can be explained by only a minor part of the area being covered by the survey and is reflected in a small number of rectangles included.

Fish density and its variation in space and time.

In order to visualize the distribution of density and temperature for each year as well as the development throughout the period of investigation we have presented annual maps of two of the data sets used for computation of ambient temperature. In Figures 4 and 5 distributions of echo density (all sizes) and swept area densities (fish bigger than 30 cm) are presented together with bottom temperatures. The two sets of maps show similarity as to the main development; an extension of the distribution area towards east and north from 1990 to 1993 following the increase in temperature during 1989 demonstrated in Figure 3 as well as by the eastward displacement of the 1 and 2°C isotherms from 1989 to 1990 (Figures 4 or 5). Regarding the areas of higher fish densities, the two types of estimates show dissimilarities which to a large extent reflect differences in availability of fish for the sampling methods (Aglen and Nakken, 1996). Fish distributed close to or at the bottom are well within reach of the bottom trawl but less accessible to the echo sounder since fish echoes cannot be distinguished from bottom echoes. On the other hand, pelagic concentrations of fish favour reliable acoustic sampling but reduce the availability to the bottom trawl. Hence, variations in the vertical density profile of fish over the area may effect the two types of density estimates differently. Also, systematic changes in the overall vertical distribution pattern from one year to another, as shown in Figure 6 for cod for 1993-1995, may reduce the comparability between these years in either type of estimate. Clearly, there was a tendency to an increasing proportion of fish close to the bottom during this period. In 1995 about 65 and 90 percent of the total acoustic recordings of cod were obtained at distances respectively less than 50 and 100m from the bottom, while the corresponding figures for 1993 were 43 and 73 percent. Bottom depth in the area of cod recordings vary mainly between 150 and 400m and most of the fish are found over depths between 200 and 300m (Korsbrekke *et al.,* 1995; Figure 3). Figure 6 thus indicates that 100m depth might be a more appropriate upper limit for computation of ambient temperature in these years.

The swept area densities may also be effected by temperature dependant capture efficiency. For a range in temperature from -1 to 6°C as observed in Figure 4 and 5 the capture efficiency will be affected in two ways (He, 1993). In the upper range, 4-6°C, large cod are capable of maintaining swimming speeds of more than 3 knots for longer than 30 minutes; the duration of a trawl haul. In the lower range, -1 to 1°C, the swimming speed of the smaller specimens, less than 20 cm in length (1 and 2 year old), will be less than the herding speed of the sweeps. These specimens will consequently be overtaken by the sweeps and not caught. The mentioned mechanisms imply that the temperature and size dependant endurance swimming ability of cod may bias the swept area estimates downwards; for large fish in the warmer south western parts of the area and for small fish in the cold eastern parts. Since swept area densities are used in the calculation of proportions of number of fish at length, p, (Equation 4) for acoustic density estimates, the latter will also be effected by these mechanisms.

The locations of the centres of mass of distribution for each age group, as calculated from each years acoustic density distribution, are enveloped in Figure 7. Older age groups were distributed farther west than the younger ones as also shown previously by Nakken and Raknes (1987) and Shevelev *et al.* (1987). A clear tendency of reduced interannual variability with age of the centre of distribution is also seen from Figure 7.

Ambient temperature and its variation

In Table 2 the relative frequency distribution of number of fish by age and bottom temperature is shown for acoustic density and in Table 3 for swept area density. Two systematic patterns, which clearly show up in both frequency distributions, should be noted. Each year the main distribution density moves downward to the right indicating that older fish were found in warmer water than younger ones. It is also seen that in some years, like 1994, the whole density distribution is skewed to the left, towards lower temperatures, in other years, like 1990, to the right, towards higher temperatures. Focusing on acoustic estimates of 3 year old cod, the median bottom temperature in 1994 is in the 0.5 to 1 °C interval, in 1990 in the interval from 4 to 4.5 °C. This large difference is also reflected in the four different ambient temperature representations given in Tables 2 and 3, although the actual size varies.

A year by year comparison of distributions of echo densities (Figure 4) with swept area densities (Figure 5) indicates that some difference in the corresponding ambient temperatures must be expected. The higher temperatures of the 100m depth to bottom interval, as compared to bottom temperature, found in most areas must also effect the ambient temperature values. A systematic study of the different categories of ambient temperature is done by regression analyses and tests (Table 4). The mean 100m depth to bottom ambient temperatures are found to be higher than those at the bottom for all ages, acoustic and trawl estimates. The mean ambient temperatures based on acoustical estimates are higher (equal in one case) than the swept area estimates at all ages and both vertical temperature levels. The differences are, however, small and not statistically significant for fish of age 1, 2 and (marginally) 3. The temporal development of the four different ambient temperature representations are shown in Figure 8 for 3 and 5 year old cod.

While the above discussion highlighted the dissimilarities of the different mean ambient temperature categories, no suggestion was given to which best represents the temperature at which the cod actually have lived. The 100m depth to bottom vertical interval was chosen to cover the whole vertical distribution area of the cod. However, Figure 6 indicates that by far the most cod are distributed from the bottom up to 100m above so that, in accordance with the discussion in the previous section, the bottom temperature is probably a more realistic choice than the vertically averaged 100m depth to bottom temperature.

Since the temperature fields used are the same there are 2 main factors that determine the difference between acoustic and trawl based ambient temperatures: Differences in the density estimates themselves and in the manner of ambient temperature calculation. Causes of differences in the two types of density estimates were discussed in the previous section. A strength of the acoustic estimates is that they are based on continuous recordings along the transects at all depth levels in addition to including information on species and size composition from trawl samples. An extra source of uncertainty enters the trawlbased ambient temperature estimates through the rather rough estimates of area within each temperature interval. This lead to ambient temperatures based on acoustic estimates and bottom temperature, hereafter termed ambient temperature, being used in all further calculations and comparisons.

Mean ambient winter temperatures for cod of ages 1, 2 and 3 are in Table 4 shown to be significantly lower than the corresponding Kola section temperatures. For ages 4 and 5 the mean differences are not statistically significant, while the ambient temperatures of 6 and 7 year old cod is higher than that of the Kola section. The same pattern is reflected in the root mean square errors of the regression analyses which are smallest for age 5, and the slope parameters of the regression without intercept parameter which gradually increase with age passing 1.0 from age 4 to 5. The situation is similar when comparing with mean bottom temperature within the ABCD region (Figure 2). Figure 8a shows how the three mean temperatures overestimate the ambient temperature of cod at age 3 the latest years, while Figure 8b indicates a much better correspondence for the 5 year old fish.

Table 4 shows that the variability in ambient temperatures is higher than that reflected in temperatures at geographically fixed areas. This is also indicated in Figure 8 and further elucidated in Figure 9 for cod of ages 3 and 5. It should be noted that the horizontal and vertical axes are equally scaled. For the periods 1978-1984 (Nakken and Raknes, 1987) and 1988-1995 the temperature average for December to February from the Kola-section varied from 2.8 to 4.5 degrees, a range of 1.7 degrees, while the ambient temperature for 3 year old cod varied from 0.6 to 5.0 degrees, a range of 4.4 degrees. For other ages the range in ambient temperature was typically somewhat smaller but not below 3.5 degrees, still more than twice that of the Kola-section. Nakken and Raknes (1987) found that the temperature variations in the Kola section reflected the variations in ambient temperature for age groups 3-8 rather effectively for the period 1979-1984. However, the 1978 data were found to fit poorly to the trend. Our results (Figure 9) show that while 1978 still may seem to be an odd year out for the 5 year old cod, the correlation established by Nakken and Raknes (1987) no longer seems to hold for 3 year old fish.

Figure 10 visualises what was found in Tables 2 and 3; mean ambient temperatures increase with age. This is in agreement with Nakken and Raknes (1987) who, based on studies of the years 1978-1984, concluded that age groups 3 or older maintained their relative distribution within the temperature field more or less independent of the absolute values of temperature. This is confirmed by our results which indicate that the rule holds for age groups 2 or older. Only a few occurrences of 2-year old cod being located in on average warmer water than those of age 3 were found (Tables 2 and 3).

Table 5 presents ambient temperatures by age and mean temperatures separately for each subarea. While the differences in ambient temperatures between the age groups are negligible in the small B and C areas, Figure 11 shows that in the larger and less homogenous D area the pattern of younger fish in colder water is distinct, with 1989 as the most notable exception. The temporal development within subarea D is also marked and comparable to that of the whole sea (Figure 12a).

All ambient and mean temperatures dealt with in this work have been for the winter, mainly February. But what is the connection between these temperatures and annual ambient temperatures? As mentioned in the introduction the seasonal migrations of cod increase in range with age. The fish will be at its south- and westernmost location in March-May and at its north- and easternmost location in September-October (Mehl *et al.* 1985). For fish of age 3 years and older this pattern implies that the seasonal migration covers an increasing range in temperature with age (Figure 1). It further implies that the seasonal variation in ambient temperature is mainly determined by the migrations and to a lesser extent by the rather limited seasonal temperature variation in fixed points. Consequently, during the annual cycle cod experience the higher temperatures in March-May and the lower in September-October. For the smaller fish (ages 1 and 2 years) which undertake insignificant or very limited seasonal migrations, the annual mean ambient temperature will not differ much from our estimates. However, for larger fish and particularly for 6 and 7 year olds which feed for several months along the polar front in waters of -1 to 2 °C the annual means might be significantly below the values estimated by us for February.

The present investigation includes only parts of the Svalbard component of the stock. That component inhabits the waters to the north of the western parts of our area of investigation (Figures 1 and 2) and it makes up about 10-40 percent of the total abundance, varying from year class to year class (Aglen and Nakken, 1996). In this area there is a southward (winter) and northward (summer) migration (Figure 1) and to a large extent a deep water (winter)- shallow water (summer) movement associated with the cooling and heating of waters on the shallow areas of the Spitsbergen bank (Mehl *et al.* 1985). These migrations will generate seasonal variations in ambient temperature similar to those described above for the Barents Sea component. It also implies that portions of the Svalbard component in February will be inside our area of investigation particularly after 1993 when the area was extended. For fish of ages 4-7 which undertake long distance seasonal migrations we assume that our observations and findings are representative for the total number at age, but regarding the smaller fish probably about 20-30 percent of the total abundance were not included in the present investigations.

Comparison of fish distribution patterns and temperature

Figure 12 shows the development of ambient temperatures (a) and the location of the fish as represented by the longitude of the centre of mass of distribution (b) of each age group for the years 1988-1995. In 1988-1989 a slight decrease in sea temperature coincided with eastward displacements for all age groups except for the 1 and 2 year old fish. During 1990-1993/94 an eastward shift of all age groups, particularly age 3 and younger, occurred in concurrence with a decrease in mean ambient temperature. During this period the Kola section temperature as well as the mean temperature for the ABCD area indicated high but gradually decreasing temperature in the Barents Sea. The outstandingly high ambient temperatures for all age groups in 1990 (Figures 10 and 12a) can be explained as a combination of a rapid increase in temperature during the first half of 1989 throughout the southern Barents Sea (Loeng *et al.*, 1992) and a westerly cod distribution (Figures 4 and 5). Several factors accounted for the westerly distribution of the fish. The previous years had been cold (Loeng *et al.*, 1992), typically shifting the cod distribution towards the southwest (Midttun *et al.*, 1981), and older cod dominated the stock due to several years with weak recruitment (Anon., 1996). The downward trend found in mean ambient temperature of all age groups, but particularly 1-3 following the 1990 maximum can partly be explained by the survey coverage until 1992 being restricted to the ABCD area (Figure 2). This is expected to have lead to the ambient temperatures of the younger, most easterly distributed, age groups being overestimated prior to 1993, since fish east of ABCD and thus in colder waters were not recorded and included in the estimates.

In the period from 1993-1995 the distribution of the two youngest age groups again showed a somewhat different pattern than the others. The centre of mass of distribution shifted westwards as the sea temperature decreased, thereby reducing the significant drop in ambient temperature from 1993 to 1994 as seen for the other age groups. The low ambient temperatures experienced by the older age groups in 1994 seems to have lead to a more westerly distribution the year after.

Our results of east-west displacements of Northeast arctic cod in connection with varying water temperature in the Barents Sea support the results of earlier authors, notably Midtun *et al.* (1981), Nakken and Raknes (1987) and Shevelev *et al.* (1987) and are also similar to those from other waters (Rose *et al.*, 1994). Whether these variations in horizontal distribution can be regarded as a response to temperature alone, to other related environmental factors (abiotic and biotic) or to abundance, i. e. a simple need for space, remains illusive. Shevelev *et al.* (1987), who studied the 1974-1981 year classes, hypothesized that the response to changes in water temperature occurs through temperature induced changes in distribution of prey organisms.

The distribution of a year class of cod could also, to a large degree, be determined during the first half year of life when larvae and 0-group are transported by the current system from the spawning grounds into the Barents Sea. A year with enhanced inflow of Atlantic water would normally be warmer than average and would also advect the pelagic 0-group cod further eastwards into the Barents Sea. Baranenkova (1957) and Maslov (1944 and 1960) described the 1 year old cod to remain close to were they bottom-settled in autumn as 0-group. Thus an easterly 0-group distribution would lead to an easterly distribution of the 1-group which again could influence the distribution of the year-class at older ages. Figure 12b does, however, not give any strong support or evidence for this scheme, the connection between the distribution at age 1 and 2 and that of 3 year old cod is weak. It should be noted that the centre of mass for the years 1988-1992 is computed from fish distributions inside the standard area ABCD only. In those years fish of age 3 and younger were recorded and caught at the eastern boundary of the standard area and consequently the estimated longitude might be to low and the ambient temperatures to high especially for the warm years of 1990-1992.

From Figure 12b it appears that the longitudinal location of the 1-3 year old cod gradually became more similar from 1992 to 1995 and also that the 2 year old fish in these years were located slightly further east than the 1 year olds. Such a development might be caused by temporal and geographical variations in predation on these small fish from large cod. According to Anon. (1996b) cannibalism on ages 0-3 increased considerably from 1991 to 1993/1994. In 1991 cannibalism accounted for an annual mortality rate of about 0.1 for these ages while in 1993 and 1994 it generated annual mortality rates of 2.4 (1 year olds), 0.5-0.7 (2 year olds) and 0.5-0.8 (3 year olds). It is likely that this increase in predation was more pronounced in areas of extensive overlap between prey and predator, i. e. the more western parts of the distribution area of the small fish. Thus the densities in these areas would be reduced at a faster rate than farther east. Cannibalism may thus have counteracted the westward displacement with age of ages 1 to 3 of the year classes 1991 to 1993.

Comparisons of the abundance, the longitudinal location and ambient temperature as well as the sea temperature (Kola section) are made in Figure 13 for 3 year old cod. Figure 13 shows that an increasingly eastward location of 3 year old cod, from 1990 to 1994, coincided with a decrease in the ambient temperature of this age group, as also shown in Figure 12, and with an increase in abundance. The eastward displacement during this relative warm period in the Barents Sea resulted in much lower mean ambient temperatures than in the cold years of 1988-1989. From 1993 to 1994 the temperature in the Barents Sea decreased and one should expect that the fish would be more westerly distributed in 1994 than in previous years, but instead the mass centre of fish aged 3 or older shifted even further to the east. This might be a result of the increasing abundance of young fish in combination with an effect of increased cannibalism as discussed above.

Although temperature seems to be an important factor influencing the horizontal distribution of cod, at high abundances the fish are distributed over a wider area, extended towards the east and thus shifting the centre of mass of distribution eastwards, apparently independent of the temperature conditions. This is in accordance with the findings by Shevelev *et al.* (1987). They found that at age 3 the more abundant year classes had the easternmost limit of distribution and that fish of such rich year classes migrated slower westwards with age than fish belonging to less abundant ones. This was accounted for as a combined effect of the regulating influence of high abundance and maturation rate which was lower in rich year classes than in poorer.

Myers and Stokes (1989) identified three different manners in which the geographical distribution of a fish population may change in response to changes in overall population size. The patterns identified where; 1. A proportional increase throughout its range, 2. A range extension in which the population increases relatively more in marginal habitats and 3. A relatively greater increase in the prime habitat, i.e. increased population density leads to higher concentration. The results of our study indicate that Northeast arctic cod respond according to the second manner with an easterly range extension, resulting in low ambient temperature, in periods with a general increase in population size.

In the Southern Barents Sea the mean temperature of the water column usually obtains its minimum in April, but in some years seasonal minimum in the bottom layers may occur as late as May or even June. The time of temperature minimum in the bottom layer and the rate of increase in temperature during hydrographical spring, seem to be the crucial factors for the start of cod feeding migrations eastwards. The second factor has also a major influence on the feeding migration route of cod eastwards in June-August (Boytsov *et al.*, 1987). They found that the availability of cod to the fisheries in June-August along the Murman coast was closely related to the longitude of the eastern boundary of the cod distribution in March as well as the increase in temperature during spring-summer in the deep water of the Kola section. This would suggest that our mean ambient temperatures and centres of mass of distribution may be a good indicator of the distribution into the early summer.

Effects on estimates of consumption by cod

In recent years the consumption by the stock of cod has been estimated annually by ICES

Atlanto-Scandian Herring, Capelin and Blue Whiting Assessment Working Group, e. g. (Anon., 1996a) as described by Bogstad and Gjøsæter (1994) and Bogstad and Mehl (in prep.). The temperatures used in these calculations 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 distribution area of the fish. The interannual variability is introduced by applying the monthly mean temperatures in the Kola section. The number of fish at age within each of the three areas is found by combining the ratio between numbers estimated by the surveys with the stock numbers estimated by VPA (Bogstad and Mehl, in prep.). Consumption by age group is thus estimated for each of the three areas and total consumption is found by summation.

Figure 14 indicates the "ambient" temperatures generated by the procedure described above as well as the range of ambient temperature as estimated by us. Both the interannual variability in mean ambient winter temperature of each agegroup and the variation between age groups is a lot larger in our estimates. For the period 1992-1995 the mean ambient winter temperature of ages 1-3 years were 1-3 °C lower than those used in the consumption estimates, a difference which would generate an upward error of 10-30 percent in the consumption estimates (Bogstad and Gjøsæter, 1994).

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REFERENCES

Aglen, A. and Nakken, O. 1996. Improving time series of abundance indices applying new knowledge. Fish. Res., xx: x-x.

Anon. 1996a. Report of the Atlanto-Scandian Herring, Capelin and Blue Whiting Working Group. ICES CM 1996/Assess:9, 150pp.

Anon. 1996b. Report of the Arctic Fisheries Working Group. ICES CM 1996/Assess:4, 311pp.

Anon. 1996c. Preliminary report of the international 0-group fish survey in the Barents Sea and adjacent waters in August-September 1996. ICES CM 1996/G:xx Ref. H, 37pp.

Aure, J., and Østensen, Ø. 1993. Hydrographic normals and long-term variations in Norwegian coastal waters. Fisken Havet No. 6, 1993: 1-75. (In Norwegian).

Baranenkova, A. S. 1957. Comparative abundance of yearclasses of the cod and haddock in the Barents

Sea according to the quantitative estimation of the young fish and the data on fisheries. Trudy PINRO, 10: 54-77. (In Russian).

Bochkov, Y. A. 1982. Water temperature in the 0-200m layer in the Kola-Meridian in the Barents Sea, 1900-1981. Sb. Nauchn. Trud. PINRO, Murmansk 46: 113-122. (In Russian).

Bogstad, B. and Gjøsæter, H. 1994. A method for estimating the consumption of capelin by cod in the Barents Sea. ICES Journal of Marine Science, 51: 273-280.

Borisov, V. M., and Elizarov, A. A. 1989. Long-term variations and abiotic conditions in the ecosystem of the Barents Sea. Journal of Fisheries Biology 35 (Sup. A): 139-144.

Boytsov, V. D., Mukhin, A. I., and Yaragina, N. A. 1987. Peculiarities of feeding migrations of the Lofoten-Barents Sea cod in the southern Barents Sea in relation to variability of environmental conditions. In The effect of oceanographic conditions on 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.

Brander, K. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). ICES Journal of Marine Science, 52: 1-10.

Dalen, J. and Nakken, O. 1983. On the application of the echo integration method. ICES CM 1983 / B:19. 30pp.

Fernø, A. and Olsen, S. 1994. Marine Fish Behaviour in Capture and Abundance Estimation. Fishing News Books. 221 pp.

Gunderson, D. R. 1993. Surveys of Fisheries Resources. John Wiley & Sons, New York. 248 pp.

Haltiner, G., and Williams, R. T. 1980. Numerical Prediction and Dynamic Meteorology. John Wiley & Sons, New York. xv+477pp.

Korsbrekke, K., Mehl, S., Nakken, O., and Sunnanå, K. 1995. Investigations on demersal fish in the Barents Sea winter 1995. Fisken Havet No. 13, 1995: 1-86. (In Norwegian).

Loeng, H., Blindheim, J., Ådlandsvik, B., and Ottersen, G. 1992. Climatic variability in the Norwegian and Barents Seas. ICES Marine Science Symposia 195: 52-61.

MacLennan, D. N., and Simmonds, E. J. 1991. Fisheries Acoustics. Chapman & Hall, London. 344 pp.

Maslov, N. A. 1944. The bottom fishes of the Barents Sea and their fisheries. Trudy PINRO, 8:3-186 (In Russian)

Maslov, N. A. 1960. Soviet Fisheries Investigations. North European Seas, Moscow. pp 185-231.

Mehl, S., O. Nakken, S. Tjelmeland and Ø. Ulltang. 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.

Midttun, L. 1989. Climatic fluctuations in the Barents Sea. Rapports et Proces-Verbaux des Reunions du Conseil International pour l'Exploration de la Mer, 188: 23-35.

Midttun, L. 1990. Surface temperatures in the Barents Sea. Polar Research 8: 11-16.

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).

Myers, R. A., and Stokes, K. 1989. Density-dependent habitat utilization of groundfish and the improvement of research surveys. ICES C.M. 1989/D:15. 7pp+10 Figs.

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.

Ottersen, G., 1991. MODgrid, a Model Oriented Data grider. Institute of Marine Research. Dep. of Marine Environment. Report no. 6, 1991. 30 pp.

Ottersen, G., Loeng, H., and Raknes, A. 1994. Influence of temperature variability on recruitment of cod in the Barents Sea. ICES Marine Science Symposia, 198: 471-481.

Ottersen, G., and Sundby, S. 1995. Effects of temperature, wind and spawning stock biomass on recruitment of Arcto-Norwegian cod. Fisheries Oceanography 4 (4): 278-292.

Ottersen, G., and Ådlandsvik, B. 1993. Climatological temperature and salinity fields for the Nordic Seas. Institute of Marine Research. Dep. of Marine Environment. Report no. 8, 1993. 121 pp.

Ponomarenko, I. Y. 1984. Survival of bottom-dwelling young cod in the Barents Sea and factors determining it. In: Proceedings of the Soviet-Norwegian Symposium on Reproduction and Recruitment of Arctic Cod, Leningrad, 25-30 September 1983. Ed. by O. R. Godø and S. Tilseth. Institute of Marine Research, Bergen.

Rose, G., Atkinson, B. A., Baird, J., Bishop, C. A., and Kulka, D. W. 1994. Changes in distribution of Atlantic cod and thermal variations in Newfoundland waters, 1980-1992. ICES Marine Science Symposia, 198: 542-552.

SAS Institute Inc. 1988. SAS/STAT User's Guide, Release 6.03 Edition. Cary, NC. 1028 pp.

SAS Institute Inc. 1992. SAS/ETS Software: Applications Guide 1, Version 6, First Edition. Time series modeling and forecasting, Financial reporting and loan analysis. Cary, NC: 380pp.

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 on 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.

Smith, G. D., 1985. Numerical Solution of Partial Differential Equations: Finite Difference Methods. Clarendon Press, Oxford. xi+337pp.

Taylor, J., 1976. CONMAP: A Computer Program for Contouring Oceanographic Data. Technical note no. 12, Marine Environmental Data Service, Canada.

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.

Table 1. Mean and standard deviation of temperature aggregated within the total area, within the ABCD areas covered each year (Fig. 2), and separately for each area A, B, C, D, D', E and F. Areas with no or insufficient coverage are noted - . Temperature difference is defined as temperature 100m to bottom - bottom temperature. N denotes the number of 1/2 degree latitude times 1 degree longitude acoustical rectangles covered.

Region	Year	N	Bottom Temperature	Temperature 100m-Bottom	Temperature Difference	SD Bottom Temperature	SD Temp. 100m-Bottom	Year	N	Bottom Temperature	Temperature 100m-Bottom	Temperature Difference	SD Bottom Temperature	SD Temp. 100m-Bottom
TOTAL	1988	142	3.53	4.00	0.47	1.43	1.26	1992	181	3.58	3.96	0.38	1.55	1.39
ABCD		124	3.77	4.12	0.35	1.34	1.24		167	3.72	4.09	0.37	1.51	1.34
A		53	3.49	4.15	0.65	1.35	1.14		48	4.37	4.73	0.37	0.84	0.75
B		18	5.69	5.80	0.11	0.38	0.27		16	6.02	5.94	-0.08	0.37	0.49
C		13	4.40	4.64	0.24	0,47	0.45		11	4.80	5.04	0.24	0.37	0.18
D		40	3.07	3.15	0.08	0.80	0.83		92	2.85	3.31	0.46	1.30	1.18
D'		-	-	-	-	-	-		-	-	-	-	-	-
E		-	-	-	-	-	-		-	-	-	-	-	-
F		16	1.86	3.34	1.49	0.84	1.06		-	-	-	-	-	-
TOTAL	1989	149	3.43	3.91	0.49	1.58	1.31	1993	271	2.87	3.31	0.44	1.69	1.58
ABCD		127	3.67	4.08	0.41	1.57	1.31		165	3.71	4.04	0.33	1.54	1.45
A		49	3.59	4.31	0.72	1.16	0.95		47	4.43	5.00	0.57	1.02	0.77
B		22	5.76	5.80	0.04	1.32	0.55		15	6.02	5.97	-0.05	0.48	0.36
C		13	4.37	4.54	0.16	0.34	0.37		11	4.59	5.07	0.48	0.48	0.16
D		43	2.47	2.79	0.32	1.01	0.73		92	2.85	3.11	0.26	1.31	1.17
D'		-	-	-	-	-	-		48	1.16	1.76	0.61	0.81	0.78
E		-	-	-	-	-	-		19	1.40	1.89	0.48	0.78	0.82
F		22	2.02	2.98	0.95	0.57	0.85		42	2.11	2.76	0.65	0.75	1.06
TOTAL	1990	109	4.64	4.80	0.16	1.22	1.14	1994	282	2.08	2.61	0.53	1.85	1.70
ABCD		108	4.66	4.82	0.16	1.20	1.12		168	2.95	3.29	0.34	1.71	1.51
A		37	4.70	5.24	0.54	1.01	0.82		49	3.86	4.31	0.44	0.98	0.77
B		18	6.35	6.18	-0.18	0.37	0.71		19	5.15	5.11	-0.04	0.43	0.35
C		14	4.92	4.91	-0.01	0.28	0.24		11	4.41	4.45	0.05	0.48	0.41
D		39	3.75	3.76	0.01	0.88	0.68		89	1.79	2.19	0.40	1.35	1.13
D'		-	-	-	-	-	-		47	-0.19	0.36	0.55	0.69	0.58
E		-	-	-	-	-	-		25	0.65	1.35	0.70	0.86	0.98
F		-	-	-	-	-	-		42	2.03	3.19	1.17	0.70	0.84
TOTAL	1991	191	3.65	4.17	0.51	1.57	1.38	1995	295	2.49	2.98	0.49	1.88	1.87
ABCD		161	3.76	4.18	0.41	1.68	1.46		167	3.53	3.92	0.39	1.53	1.42
A		49	4.39	5.05	0.66	0.88	0.70		48	4.07	4.68	0.61	0.90	0.82
B		19	6.23	6.14	-0.10	0.50	0.37		18	6.02	5.98	-0.04	0.44	0.35
C		12	5.01	5.06	0.05	0.21	0.22		12	4.34	4.95	0.61	0.76	0.13
D		81	2.62	3.06	0.44	1.36	1.09		89	2.62	2.94	0.33	1.23	1.06
D'		-	-	-	-	-	-		50	0.40	0.71	0.31	1.30	1.07
E		-	-	-	-	-	-		29	0.49	1.02	0.53	1.02	1.30
F		29	3.08	4.15	1.07	0.42	0.80		51	2.28	3.26	0.98	0.71	1.25

Table 2. Relative frequency distribution of number of fish as estimated by acoustic density, by age and bottom temperature. The two last columns show ambient temperature corresponding to each distribution and based on bottom temperature, $\bar{t}_b$, or temperatures in the 100m depth to bottom layer, $\bar{t}_p$.

Year	Age	Percentage of fish within temperature intervals (upper boundary given)																		$\bar{t}_b$	$\bar{t}_p$
		<-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	0	0	0	0	0	0	13	26	18	20	3	21	0	0	0	0	0	0	2.88	2.99
1988	2	0	0	0	0	0	7	9	18	6	19	7	32	1	1	0	0	0	0	3.16	3.51
1988	3	0	0	0	1	0	11	11	4	5	18	7	38	2	2	1	0	0	0	3.29	3.95
1988	4	0	0	0	1	0	9	16	5	9	11	7	32	4	4	2	0	0	0	3.25	4.14
1988	5	0	0	0	3	0	2	9	5	7	9	7	30	14	10	6	0	0	0	3.82	4.51
1988	6	0	0	0	6	0	0	2	4	4	9	2	25	19	15	12	1	0	0	4.13	4.67
1988	7	0	0	0	12	0	0	0	4	3	12	1	29	14	17	8	1	0	0	3.87	4.38
1989	1	0	0	0	1	0	1	2	62	3	3	6	18	1	1	1	0	0	0	2.87	3.14
1989	2	0	0	0	0	1	10	8	23	8	17	6	18	3	3	2	0	0	0	3.02	3.27
1989	3	0	0	0	0	1	8	7	21	16	14	8	16	4	2	1	0	0	0	3.01	3.38
1989	4	0	0	0	0	2	8	8	23	20	10	7	12	4	3	2	0	0	0	2.99	3.44
1989	5	0	0	0	0	1	4	5	22	13	8	8	18	8	5	4	0	1	1	3.42	3.84
1989	6	0	0	0	0	0	1	2	9	5	6	9	21	11	11	16	1	3	4	4.52	4.73
1989	7	0	0	0	0	0	1	2	5	3	5	10	20	9	11	21	1	4	9	4.98	5.04
1990	1	0	0	0	0	0	0	1	2	22	20	35	7	9	3	0	0	0	0	3.60	3.51
1990	2	0	0	0	0	0	0	0	0	3	7	31	19	23	16	1	1	0	0	4.30	4.21
1990	3	0	0	0	0	0	0	0	0	0	1	12	16	23	27	7	9	4	0	4.96	4.96
1990	4	0	0	0	0	0	0	0	0	0	1	6	11	17	35	12	11	7	0	5.23	5.21
1990	5	0	0	0	0	0	0	0	0	0	1	4	6	12	28	16	26	6	0	5.50	5.28
1990	6	0	0	0	0	0	0	0	0	0	0	2	3	7	25	16	41	4	0	5.73	5.33
1990	7	0	0	0	0	0	0	0	0	0	0	2	1	4	18	14	55	5	0	5.89	5.43
1991	1	0	2	2	6	9	2	2	11	30	19	9	1	5	1	0	0	0	0	2.52	2.98
1991	2	0	0	0	0	0	0	0	4	22	20	33	5	14	1	0	0	0	0	3.61	3.85
1991	3	0	0	0	0	0	0	0	3	10	16	16	6	30	14	2	2	2	0	4.23	4.51
1991	4	0	0	0	0	0	0	0	2	7	13	13	5	25	20	6	4	5	0	4.52	4.84
1991	5	0	0	0	0	0	0	0	2	6	11	15	4	26	22	5	4	5	0	4.57	4.84
1991	6	0	0	0	0	0	0	0	2	6	9	13	5	25	21	6	5	7	0	4.69	4.98
1991	7	0	0	0	0	0	0	0	1	6	7	9	5	26	19	7	6	12	0	4.85	5.09
1992	1	0	0	24	0	26	5	14	3	9	7	5	4	2	1	0	0	0	0	1.52	2.19
1992	2	0	0	15	0	22	10	6	2	23	13	7	1	0	0	0	0	0	0	1.83	2.41
1992	3	0	0	4	0	9	5	2	2	17	19	19	16	5	2	1	0	0	0	3.03	3.47
1992	4	0	0	1	0	2	3	1	2	13	15	19	24	12	5	2	1	0	0	3.71	4.06
1992	5	0	0	0	0	0	1	1	1	8	11	12	20	19	13	7	6	0	0	4.35	4.67
1992	6	0	0	0	0	1	1	1	1	9	11	11	15	21	13	9	7	0	0	4.40	4.73
1992	7	0	0	0	0	1	1	0	1	8	10	12	14	22	14	10	8	0	0	4.50	4.80
1993	1	3	0	7	30	20	15	8	9	4	2	1	1	0	0	0	0	0	0	1.00	1.51
1993	2	2	0	1	12	24	21	16	14	5	3	1	1	0	0	0	0	0	0	1.40	1.92
1993	3	0	0	1	3	9	9	12	14	12	10	7	13	7	3	0	1	0	0	2.73	3.17
1993	4	0	0	0	1	1	1	3	6	8	6	9	18	29	10	1	5	0	0	4.04	4.37
1993	5	0	0	0	0	1	1	2	4	5	4	6	19	36	15	2	5	1	0	4.39	4.68
1993	6	0	0	0	0	1	1	1	4	5	4	5	15	33	17	3	7	3	0	4.50	4.77
1993	7	0	0	0	0	1	2	2	5	7	4	6	12	20	19	6	11	5	0	4.53	4.77
1994	1	0	12	40	7	7	6	11	5	3	3	3	2	1	0	0	0	0	0	0.64	1.30
1994	2	0	15	8	30	21	8	11	3	1	1	1	0	0	0	0	0	0	0	0.54	1.16
1994	3	0	5	3	36	11	9	19	7	4	2	2	0	0	0	0	0	0	0	1.00	1.60
1994	4	0	3	2	13	3	4	24	14	6	8	7	5	6	2	3	0	0	0	2.30	2.80
1994	5	0	2	1	8	2	2	14	11	5	7	9	14	14	4	6	0	0	0	3.08	3.45
1994	6	0	1	1	4	1	1	10	10	6	7	9	21	18	6	4	0	0	0	3.44	3.74
1994	7	0	1	1	1	1	1	9	9	6	7	7	20	24	10	3	0	0	0	3.68	4.01
1995	1	3	3	15	7	2	8	17	8	15	8	5	5	3	0	0	0	0	0	1.83	2.35
1995	2	1	1	12	6	4	14	24	5	18	9	3	1	0	0	0	0	0	0	1.67	2.21
1995	3	0	1	5	2	0	11	13	10	18	20	14	4	2	0	0	0	0	0	2.50	2.99
1995	4	0	0	0	1	0	3	4	13	15	21	23	12	7	0	1	1	0	0	3.30	3.86
1995	5	0	0	0	0	0	1	1	8	15	14	22	18	13	1	3	4	0	0	3.73	4.34
1995	6	0	0	0	0	0	1	1	7	17	10	20	17	13	1	6	7	1	0	3.94	4.59
1995	7	0	0	0	0	0	0	0	7	18	8	20	16	13	1	7	8	0	0	3.98	4.65

Table 3. Relative frequency distribution of number of fish as estimated by swept area density by age and bottom temperature. The two last columns show ambient temperature corresponding to each distribution and based on bottom temperature, $\bar{t}_b$, or temperatures in the 100m depth to bottom layer, $\bar{t}_p$.

Year	Age	Percentage of fish within temperature intervals (upper boundary given)																		$\bar{t}_b$	$\bar{t}_p$
		< -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	0	0	0	0	0	0	9	30	8	20	30	2	0	0	0	0	0	0	2.95	3.40
1988	2	0	0	0	0	0	3	3	4	4	7	12	37	29	0	0	0	0	0	3.93	4.31
1988	3	0	0	0	0	0	10	5	6	5	11	24	22	15	0	0	0	0	0	3.45	3.99
1988	4	0	0	0	0	0	17	4	16	5	6	22	15	10	3	1	0	0	0	3.16	3.98
1988	5	0	0	0	0	0	7	3	17	5	6	19	18	11	11	2	1	0	0	3.61	4.32
1988	6	0	0	0	0	0	1	1	15	1	7	10	15	10	32	6	3	0	0	4.28	4.75
1988	7	0	0	0	0	0	0	1	13	0	11	13	17	12	24	7	3	0	0	4.25	4.72
1989	1	0	1	2	1	4	22	12	19	10	8	5	10	3	1	2	0	0	0	2.41	2.71
1989	2	0	0	5	2	3	5	13	12	11	17	9	14	3	2	2	1	0	0	2.80	3.04
1989	3	0	0	21	2	3	7	11	13	5	12	14	9	2	1	0	0	0	0	2.19	2.53
1989	4	0	0	24	2	4	5	17	14	6	9	5	8	3	1	1	0	0	0	1.93	2.51
1989	5	0	0	10	2	3	3	19	13	9	7	5	15	9	2	3	1	1	0	2.74	3.51
1989	6	0	0	1	1	1	1	10	7	9	5	7	22	14	8	9	4	2	0	3.89	4.66
1989	7	0	0	0	1	1	0	7	5	8	6	6	20	12	13	13	7	2	0	4.29	5.03
1990	1	3	4	1	0	5	7	4	16	23	16	11	5	3	2	0	0	0	0	2.52	2.78
1990	2	0	0	0	0	0	0	1	3	12	16	19	20	14	12	0	1	0	0	3.89	4.09
1990	3	0	0	0	0	0	0	0	1	4	6	11	32	22	14	5	5	1	0	4.51	4.73
1990	4	0	0	0	0	0	0	0	1	2	3	9	28	26	15	8	5	2	0	4.66	4.93
1990	5	0	0	0	0	0	0	0	2	2	2	8	21	22	12	20	8	3	0	4.88	5.08
1990	6	0	0	0	0	0	0	0	1	1	1	5	13	15	12	34	14	4	0	5.24	5.32
1990	7	0	0	0	0	0	0	0	1	1	1	3	9	9	9	37	25	4	0	5.49	5.51
1991	1	0	3	13	12	7	16	4	12	21	11	0	1	0	1	0	0	0	0	1.59	2.16
1991	2	0	1	1	1	2	16	1	20	26	23	3	4	1	1	0	0	0	0	2.59	3.01
1991	3	0	0	0	0	0	1	0	5	18	27	9	7	10	19	1	1	2	0	3.85	4.34
1991	4	0	0	0	0	0	0	0	3	12	18	8	6	10	31	4	3	5	0	4.40	4.87
1991	5	0	0	0	0	0	0	0	3	12	24	6	6	9	32	3	3	3	0	4.27	4.84
1991	6	0	0	0	0	0	0	0	3	10	14	6	8	8	38	4	4	5	0	4.52	5.03
1991	7	0	0	0	1	0	0	0	4	11	11	5	7	8	36	4	6	6	0	4.56	5.09
1992	1	0	0	8	6	6	3	24	8	7	11	13	7	6	2	1	0	0	0	2.42	2.95
1992	2	0	0	1	4	2	2	11	26	8	14	29	2	1	0	0	0	0	0	2.72	3.02
1992	3	0	0	0	1	1	3	6	5	8	17	33	13	10	3	1	0	0	0	3.50	3.79
1992	4	0	0	0	0	1	2	4	3	8	13	22	17	19	7	2	1	0	0	3.85	4.22
1992	5	0	0	0	0	0	1	1	2	5	11	14	19	20	14	6	7	0	0	4.35	4.85
1992	6	0	0	0	0	0	1	2	3	6	12	13	16	18	14	7	8	0	0	4.32	4.83
1992	7	0	0	0	0	0	1	1	3	5	11	13	14	19	16	8	9	0	0	4.42	4.88
1993	1	0	0	1	10	8	26	25	13	5	4	2	2	2	0	1	0	0	0	1.72	1.95
1993	2	0	0	2	8	22	18	27	10	7	4	2	0	0	0	0	0	0	0	1.52	1.80
1993	3	0	0	0	4	20	10	9	14	13	16	6	4	2	1	0	0	0	0	2.20	2.62
1993	4	0	0	0	2	6	3	5	12	13	11	12	16	12	6	1	2	1	0	3.34	3.75
1993	5	0	0	0	1	2	1	2	4	11	10	13	18	19	10	2	5	2	0	4.00	4.38
1993	6	0	0	0	2	2	1	3	7	11	8	11	14	19	9	3	7	3	0	4.04	4.38
1993	7	0	0	0	2	2	1	2	3	10	7	12	14	16	9	5	12	6	0	4.35	4.54
1994	1	0	11	17	12	17	7	9	9	3	6	4	2	2	1	0	0	0	0	1.13	1.59
1994	2	0	18	17	17	16	11	8	6	3	2	1	0	0	0	0	0	0	0	0.63	1.12
1994	3	0	10	12	10	16	14	21	10	2	2	2	1	0	0	0	0	0	0	1.03	1.53
1994	4	0	2	4	4	9	13	23	24	3	5	6	4	2	1	0	0	0	0	1.96	2.43
1994	5	0	1	2	2	4	10	16	21	4	6	10	9	7	5	1	0	0	0	2.64	3.07
1994	6	0	1	2	1	2	7	14	16	5	6	14	12	9	10	1	0	0	0	3.08	3.45
1994	7	0	1	2	2	1	6	14	14	6	7	16	12	10	7	2	0	0	0	3.10	3.45
1995	1	0	6	12	6	5	21	17	9	12	5	2	3	2	1	0	0	0	0	1.53	2.05
1995	2	0	4	8	9	6	16	27	11	12	4	1	0	0	0	0	0	0	0	1.49	2.02
1995	3	0	2	2	5	4	7	25	12	18	13	10	2	1	0	0	0	0	0	2.23	2.69
1995	4	0	0	0	0	0	14	20	12	13	16	13	6	5	1	1	0	0	0	2.72	3.17
1995	5	0	0	0	0	0	16	14	9	9	13	10	10	10	3	5	1	0	0	3.09	3.61
1995	6	0	0	0	0	0	13	7	11	9	13	9	10	12	6	9	2	0	0	3.45	4.05
1995	7	0	0	0	0	0	7	3	15	10	15	9	12	13	5	9	3	0	0	3.64	4.25

Table 4. Comparison of ambient and mean temperatures by regression analyses and paired t-tests.
R^2 is the determination coefficient, RMSE the root mean square error, and p the two-sided probability value.

			With intercept				No intercept		Paired t-test	
Dependent	Independent	Age	Intercept	Slope	R^2	RMSE	Slope	RMSE	Mean Difference	p
Acoustic, bottom	Acoustic, 100m-bottom	1	-1.08	1.28	0.98	0.17	0.88	0.37	-0.39	0.00
		2	-0.94	1.20	0.99	0.12	0.90	0.35	-0.37	0.00
		3	-0.91	1.14	0.98	0.16	0.90	0.30	-0.41	0.00
		4	-1.16	1.18	0.94	0.24	0.90	0.30	-0.42	0.00
		5	-1.49	1.26	0.91	0.25	0.93	0.30	-0.34	0.01
		6	-1.94	1.36	0.84	0.29	0.94	0.32	-0.27	0.04
		7	-2.81	1.54	0.89	0.26	0.95	0.35	-0.24	0.09
Acoustic, bottom	Trawl, bottom	1	-0.21	1.14	0.48	0.78	1.04	0.74	0.07	0.79
		2	0.12	0.95	0.76	0.67	0.99	0.62	0.00	0.99
		3	0.32	0.97	0.87	0.45	1.06	0.43	0.22	0.18
		4	0.95	0.83	0.86	0.38	1.10	0.45	0.41	0.02
		5	0.80	0.89	0.92	0.24	1.10	0.28	0.41	0.00
		6	0.63	0.92	0.85	0.28	1.07	0.27	0.32	0.01
		7	0.59	0.93	0.80	0.35	1.06	0.34	0.27	0.05
Acoustic, 100m-bottom	Trawl, 100m-bottom	1	0.34	0.88	0.45	0.64	1.01	0.60	0.05	0.83
		2	0.43	0.85	0.79	0.52	0.99	0.51	0.02	0.93
		3	0.61	0.88	0.89	0.36	1.05	0.39	0.23	0.11
		4	1.35	0.73	0.87	0.29	1.08	0.43	0.36	0.03
		5	1.33	0.74	0.89	0.21	1.05	0.30	0.24	0.04
		6	1.48	0.70	0.86	0.18	1.02	0.25	0.13	0.16
		7	1.78	0.64	0.82	0.20	1.01	0.30	0.09	0.43
Trawl, bottom	Trawl, 100m-bottom	1	-0.44	1.01	0.95	0.14	0.84	0.17	-0.42	0.00
		2	-0.51	1.06	0.99	0.11	0.90	0.22	-0.35	0.00
		3	-0.53	1.04	0.99	0.11	0.89	0.20	-0.41	0.00
		4	-0.66	1.05	0.98	0.17	0.88	0.23	-0.48	0.00
		5	-0.88	1.09	0.96	0.18	0.88	0.23	-0.51	0.00
		6	-0.78	1.07	0.91	0.21	0.90	0.22	-0.46	0.00
		7	-0.63	1.05	0.89	0.25	0.91	0.24	-0.42	0.00
Acoustic, bottom	Mean Kola,, Dec.-Feb.	1	1.56	0.14	0.00	1.11	0.53	1.04	-1.85	0.00
		2	-0.28	0.69	0.06	1.34	0.62	1.24	-1.51	0.01
		3	-2.79	1.49	0.31	1.06	0.79	1.03	-0.87	0.04
		4	-3.04	1.69	0.66	0.58	0.93	0.64	-0.29	0.22
		5	-1.70	1.47	0.73	0.43	1.04	0.44	0.15	0.39
		6	0.97	0.87	0.34	0.58	1.11	0.55	0.46	0.05
		7	1.49	0.77	0.22	0.68	1.14	0.66	0.57	0.04
Acoustic, bottom	Bottom ABCD	1	-4.28	1.72	0.61	0.69	0.58	0.84	-1.61	0.00
		2	-5.94	2.25	0.68	0.78	0.68	1.03	-1.28	0.01
		3	-5.59	2.33	0.85	0.49	0.85	0.83	-0.63	0.05
		4	-2.79	1.73	0.77	0.48	1.00	0.57	-0.06	0.79
		5	-1.31	1.46	0.79	0.37	1.10	0.38	0.39	0.03
		6	-0.64	1.36	0.91	0.21	1.19	0.21	0.70	0.00
		7	-0.36	1.32	0.73	0.41	1.22	0.38	0.81	0.00

Table 5. Ambient temperatures by area and age 1988-1995 from acoustic estimates and bottom temperature. Areas with no or insufficient coverage are noted - . The rightmost column shows the corresponding mean temperatures.

Year	Area	No. cells	Ambient temperature by age							Mean temperature
			1	2	3	4	5	6	7	
1988	A	53	-	3.3	3.2	3.3	3.8	3.9	3.9	3.49
1988	B	18	-	-	5.7	5.6	5.5	5.5	5.4	5.69
1988	C	13	4.1	4.3	4.4	4.4	4.5	4.5	4.5	4.40
1988	D	40	2.8	3.1	3.8	3.9	4.0	4.0	4.0	3.07
1988	F	16	-	1.6	1.7	1.8	1.9	1.7	1.5	1.86
1989	A	49	2.7	3.3	3.4	3.4	3.7	4.0	4.2	3.59
1989	B	22	5.6	5.5	5.7	6.0	6.1	6.2	6.5	5.76
1989	C	13	4.4	4.3	4.3	4.3	4.3	4.4	4.3	4.37
1989	D	43	2.5	2.8	2.7	2.6	2.5	2.6	2.8	2.47
1989	F	22	1.7	1.5	1.6	1.6	1.9	2.4	2.6	2.02
1990	A	37	4.6	4.6	5.2	5.3	5.3	5.3	5.4	4.70
1990	B	18	6.1	6.0	6.1	6.1	6.2	6.2	6.2	6.35
1990	C	14	5.0	4.8	4.9	5.1	5.2	5.2	5.2	4.92
1990	D	39	3.5	4.1	4.3	4.4	4.4	4.4	4.3	3.75
1991	A	49	4.4	4.2	4.8	4.9	4.9	5.0	5.0	4.39
1991	B	19	5.9	6.5	6.2	6.2	6.2	6.3	6.3	6.23
1991	C	12	4.9	5.0	5.0	5.0	5.0	5.0	5.0	5.01
1991	D	81	2.3	3.6	4.0	4.0	4.0	4.0	4.1	2.62
1991	F	29	2.9	3.1	3.2	3.2	3.2	3.1	3.1	3.08
1992	A	48	3.6	3.6	4.0	4.1	4.3	4.4	4.5	4.37
1992	B	16	5.6	5.9	5.9	5.9	6.0	6.1	6.1	6.02
1992	C	11	4.8	4.7	4.7	4.8	4.9	4.9	5.0	4.80
1992	D	92	1.1	1.8	2.6	3.1	3.4	3.4	3.5	2.85
1993	A	47	3.7	4.2	4.4	4.7	4.7	4.7	4.8	4.43
1993	B	15	5.8	5.8	5.8	5.8	5.8	5.8	5.8	6.02
1993	C	11	4.7	4.7	4.7	4.8	4.8	4.7	4.7	4.59
1993	D	92	1.2	1.5	2.5	3.6	3.8	3.8	3.5	2.85
1993	D'	48	0.6	1.3	1.4	1.3	1.3	1.3	1.2	1.16
1993	E	19	0.7	0.8	1.3	1.8	1.9	1.9	1.9	1.40
1993	F	42	1.8	2.0	2.5	2.6	2.7	2.7	2.7	2.11
1994	A	49	3.6	3.5	3.4	3.7	4.0	4.1	4.4	3.86
1994	B	19	5.0	5.0	5.0	5.3	5.2	5.0	5.1	5.15
1994	C	11	4.3	4.2	4.3	4.4	4.5	4.4	4.4	4.41
1994	D	89	1.1	0.6	0.9	1.7	2.0	2.3	2.6	1.79
1994	D'	47	-0.1	-0.1	0.0	-0.0	-0.2	-0.3	-0.4	-0.19
1994	E	25	-0.0	0.7	1.3	0.8	0.8	1.1	1.3	0.65
1994	F	42	1.7	1.4	1.9	2.1	2.3	2.4	2.7	2.03
1995	A	48	3.7	3.6	3.5	3.7	4.0	4.0	4.0	4.07
1995	B	18	6.0	5.9	5.9	5.9	6.0	6.0	6.0	6.02
1995	C	12	4.2	4.1	4.2	4.1	4.2	4.2	4.1	4.34
1995	D	89	1.8	1.7	2.5	3.3	3.5	3.6	3.7	2.62
1995	D'	50	1.0	1.8	1.7	0.6	0.6	0.6	0.6	0.40
1995	E	29	1.0	1.1	1.4	1.8	1.6	-	-	0.49
1995	F	51	2.0	1.9	2.1	2.4	2.7	2.7	2.7	2.28

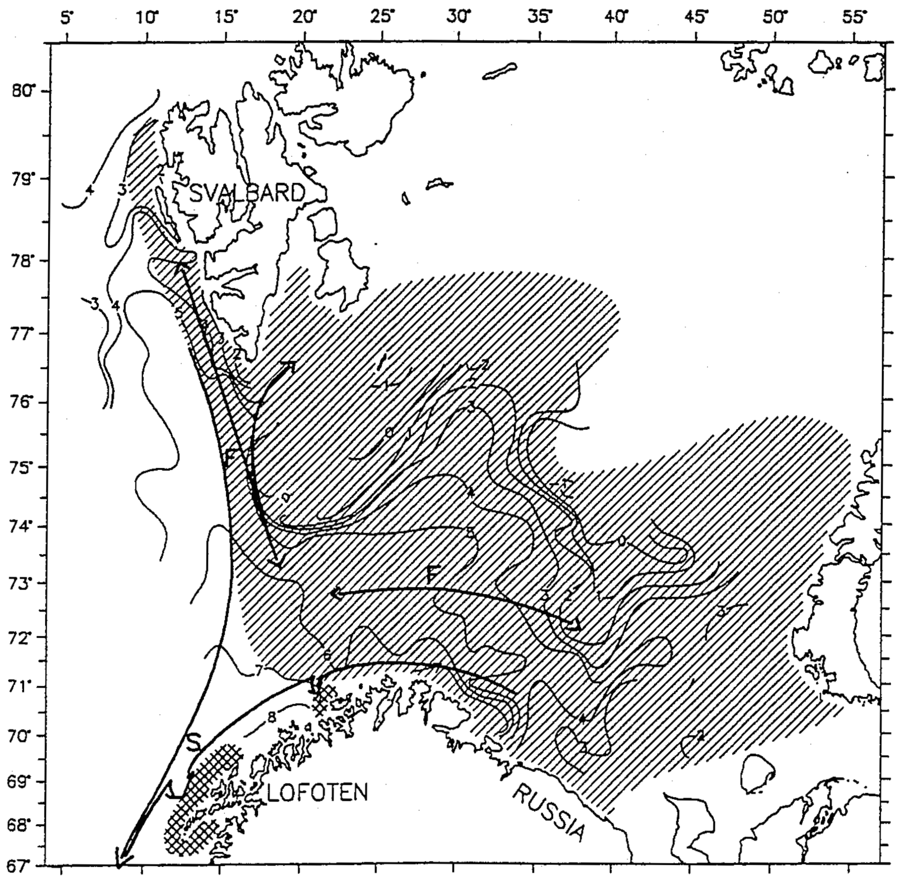


Figure 1. The area of distribution of Northeast Arctic cod and isotherms (T °C) at 100 m depth. Feeding areas (hatched), spawning areas (cross hatched), seasonal feeding migrations (F) and spawning migrations (S) are indicated (after Mehl, 1991). Temperature distribution is for August 1995 (Anon. 1996c).

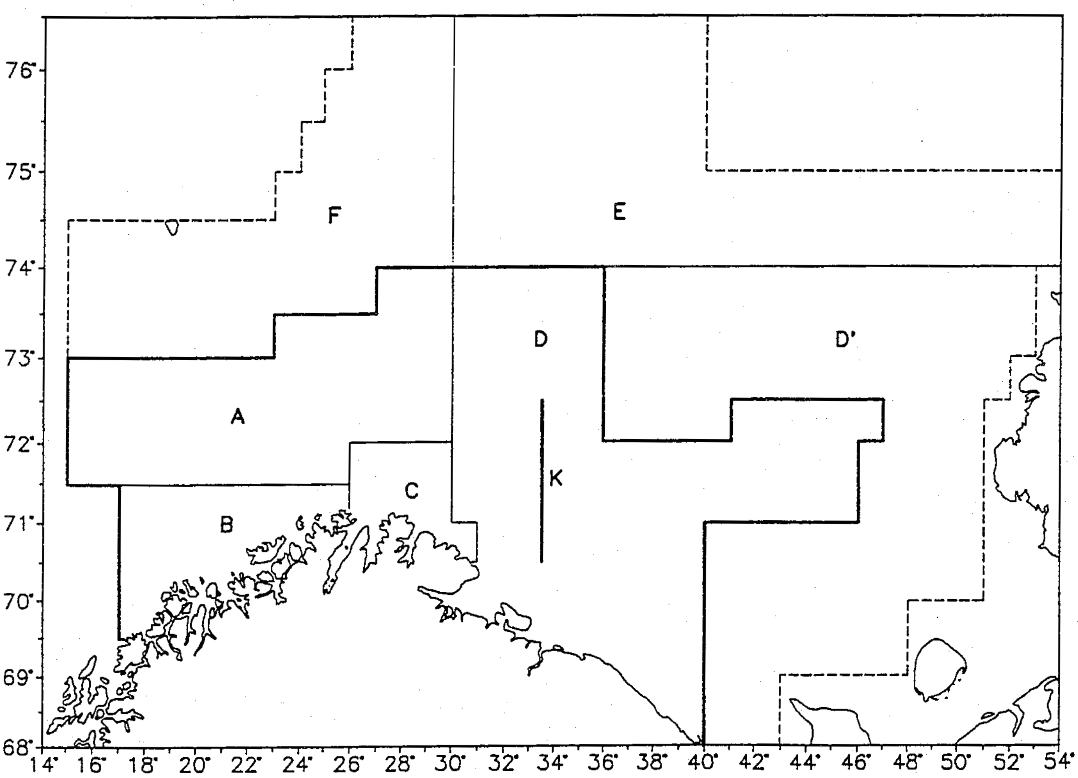


Figure 2. The survey area. Subareas for calculating indices of abundance and average temperature are framed. The part of the Kola section for which mean temperatures are established is shown.

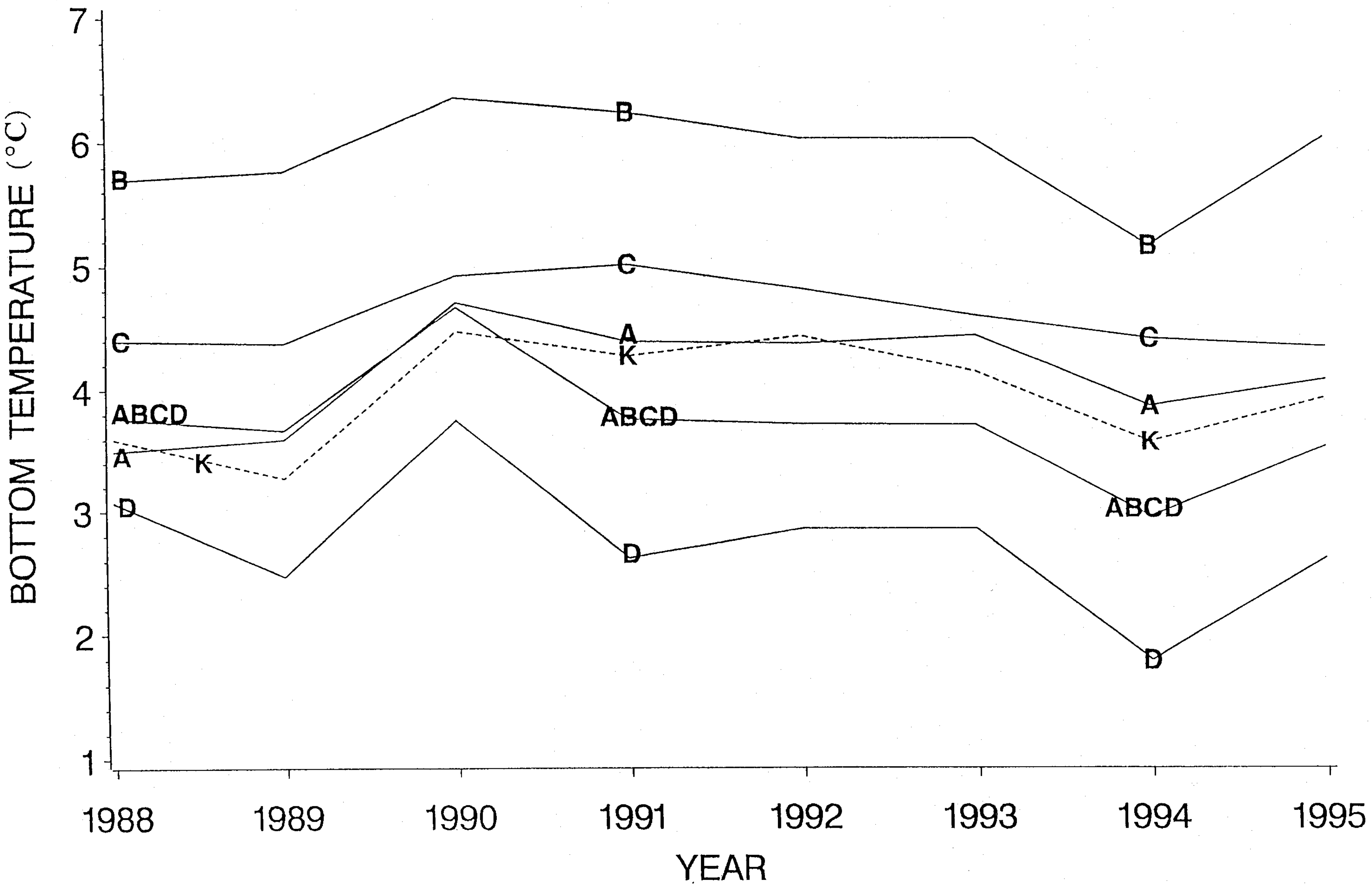


Figure 3. Average bottom temperature (T °C), in February 1988-1995 in subareas A, B, C and D, in ABCD as a whole and in the Kola section (K).

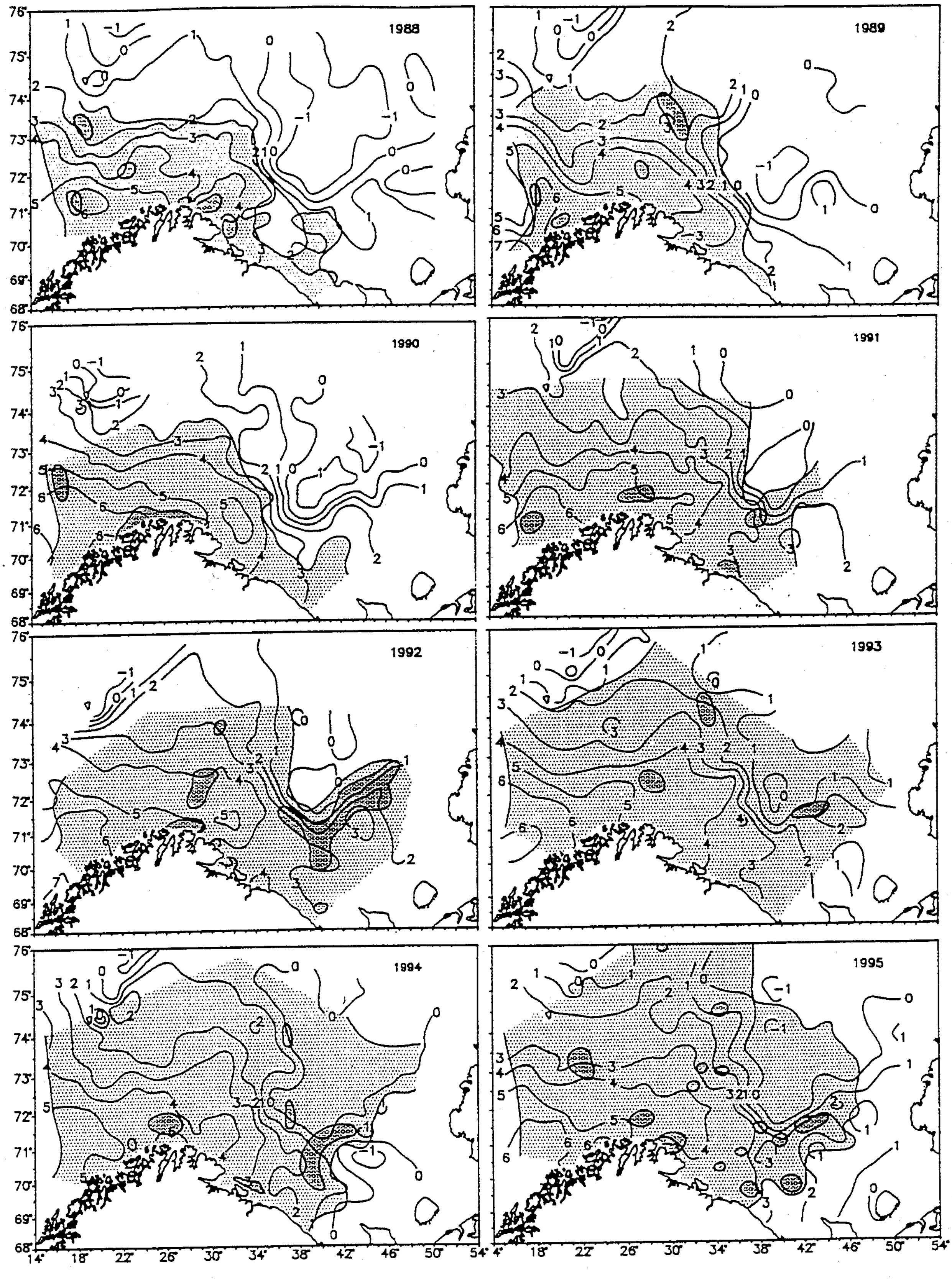


Figure 4. Distribution of echo densities (back scattering coefficient, s_A) of cod (shaded areas) and bottom temperature (isotherms, T °C) in February 1988-1995. Dark shading for $s_A > 100$ m^2/ (nautical mile)^2.

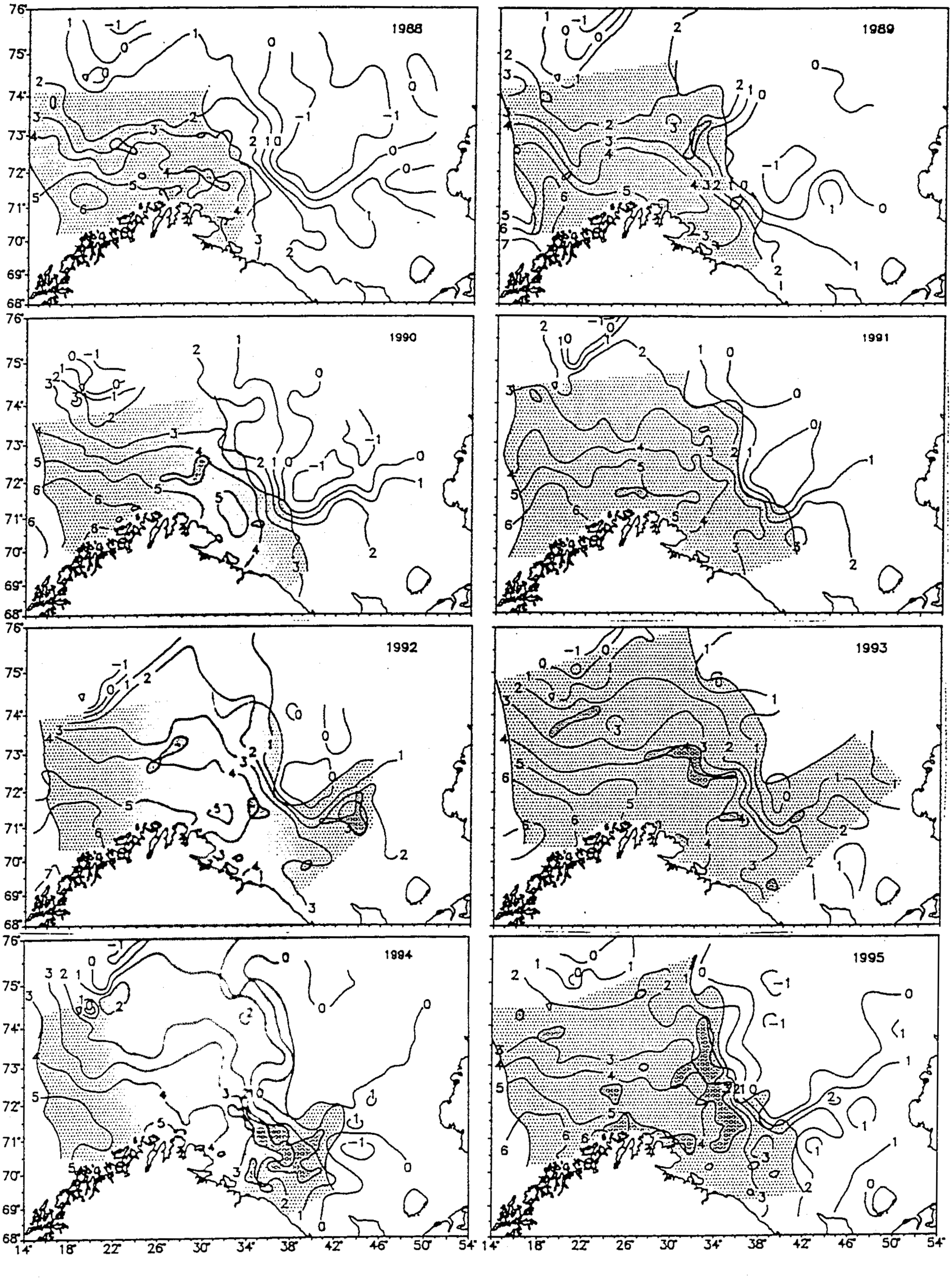


Figure 5. Distribution of swept area densities (p) of cod >30 cm in length (shaded areas) and bottom temperature (isotherms, T °C). Dark shading for p>10000 specimens/ (nautical mile)^2.

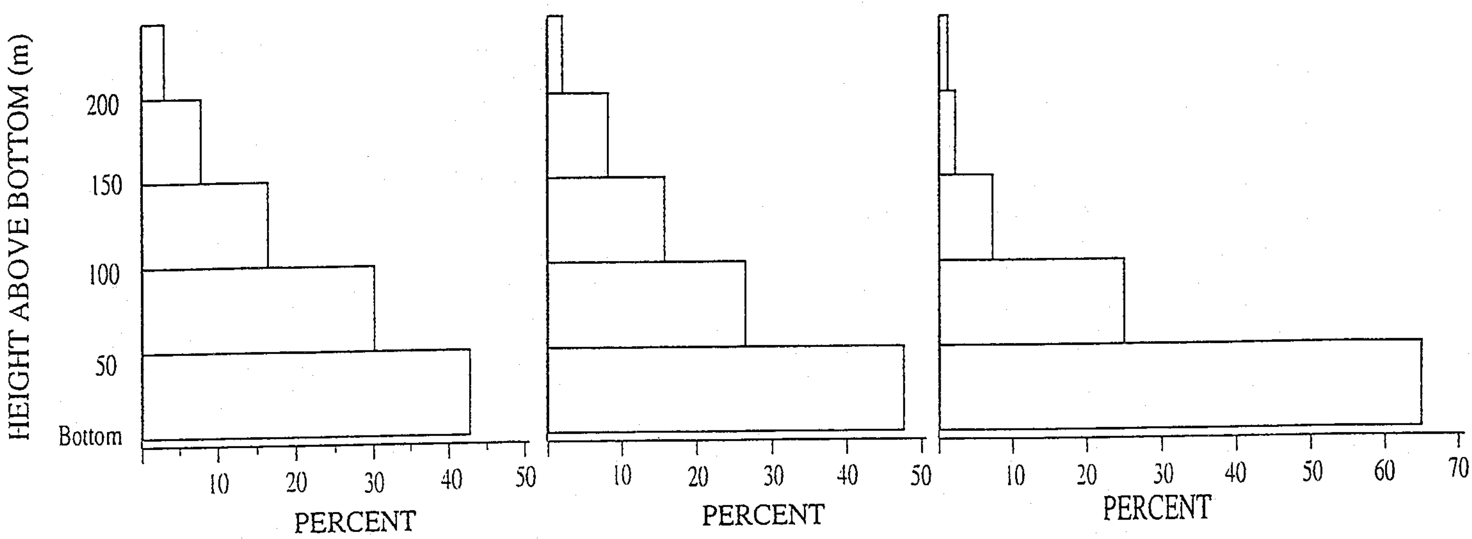


Figure 6. The vertical distribution of cod relative to the bottom in February 1993-1995. Horizontally accumulated s_A-values in 50 m height intervals given as percent of total (from Korsbrekke *et al.* 1995).

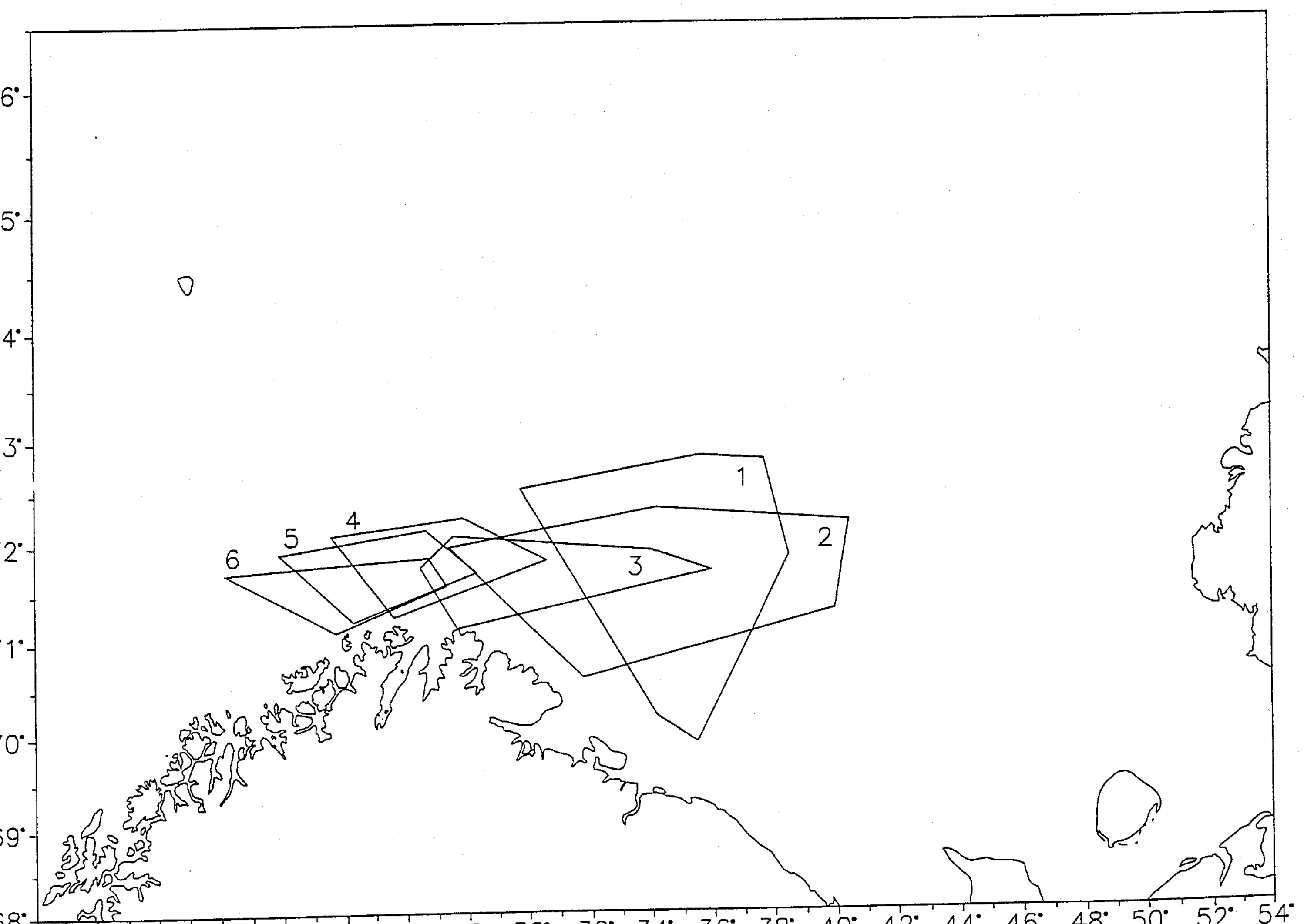
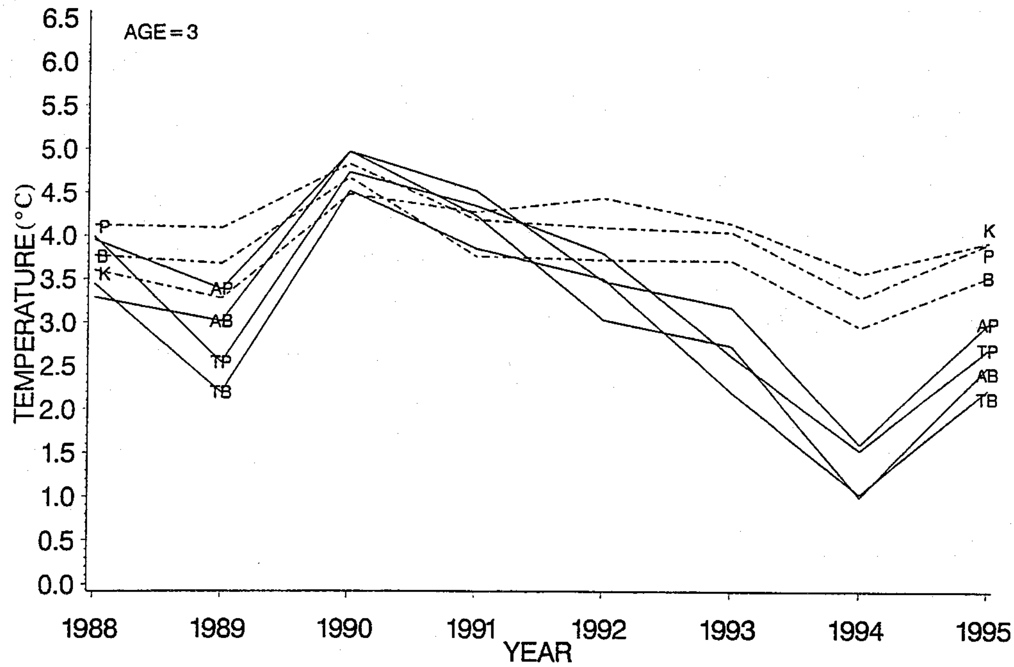


Figure 7. Areas within which the centre of mass of distribution of each age group were located 1988-1995.



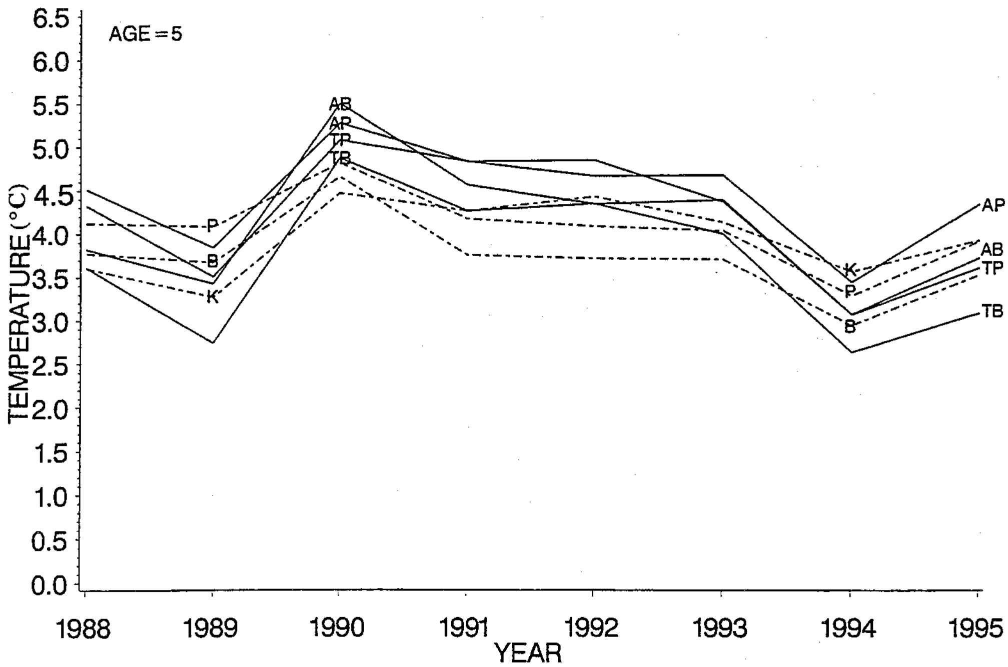


Figure 8. Mean ambient temperatures of 3 year old cod (upper panel) and 5 year old cod (lower panel) in February 1988-1995 based on acoustic estimates and temperatures 100m-bottom (AP), trawl estimates and temperatures 100m-bottom (TP), acoustic estimates and bottom temperatures (AB) and trawl estimates and bottom temperatures (TB). Mean temperatures at 0-200m in the Kola section (K), in area ABCD at the bottom (B) and 100m to bottom (P) are also shown (stippled lines).

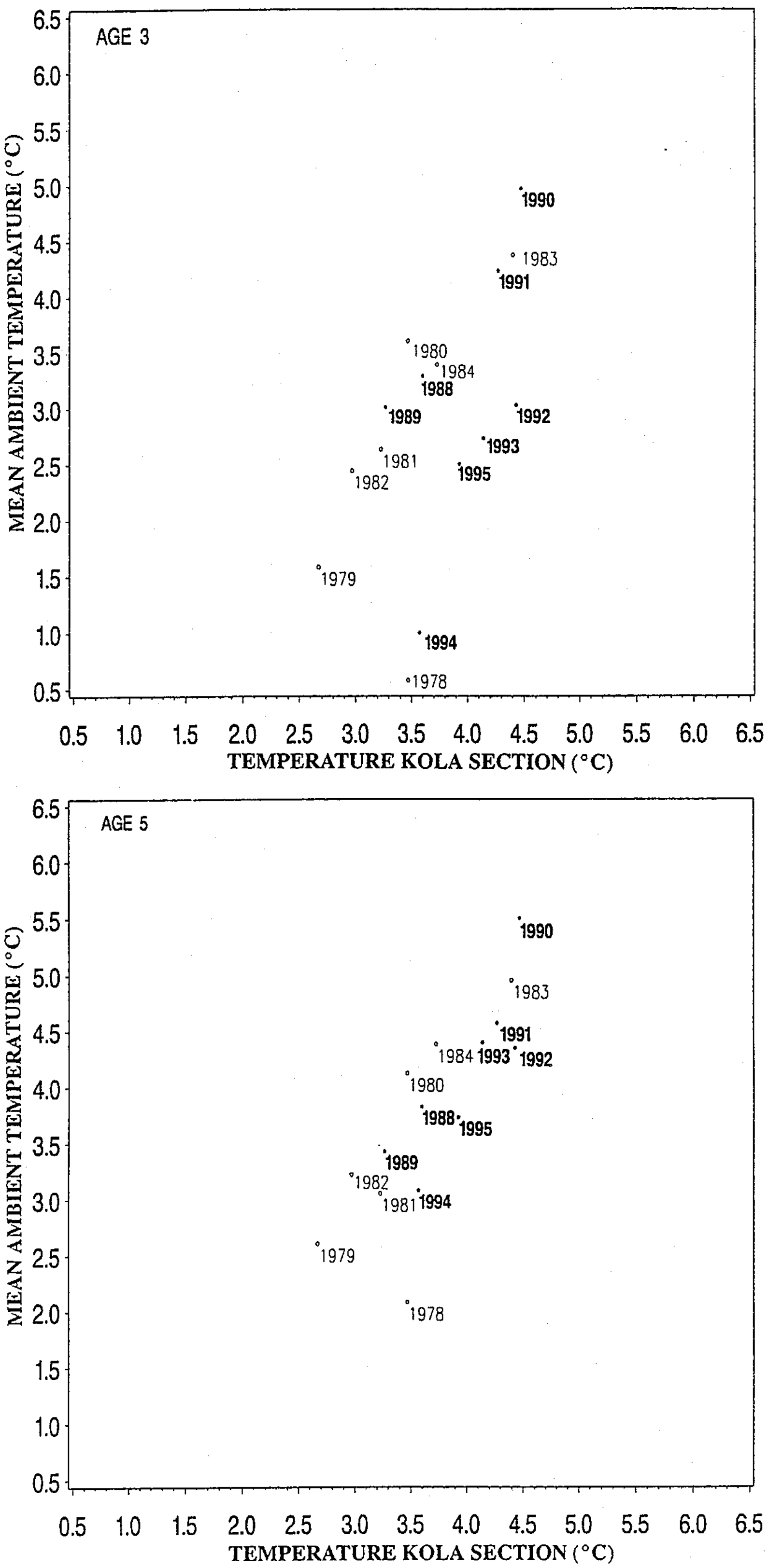


Figure 9. Mean ambient temperatures of 3 year old cod (upper panel) and 5 year old cod (lower panel) plotted against mean temperature in the Kola section. Years 1978-1984, shown with open circles and thin font, are from Nakken and Raknes (1987).

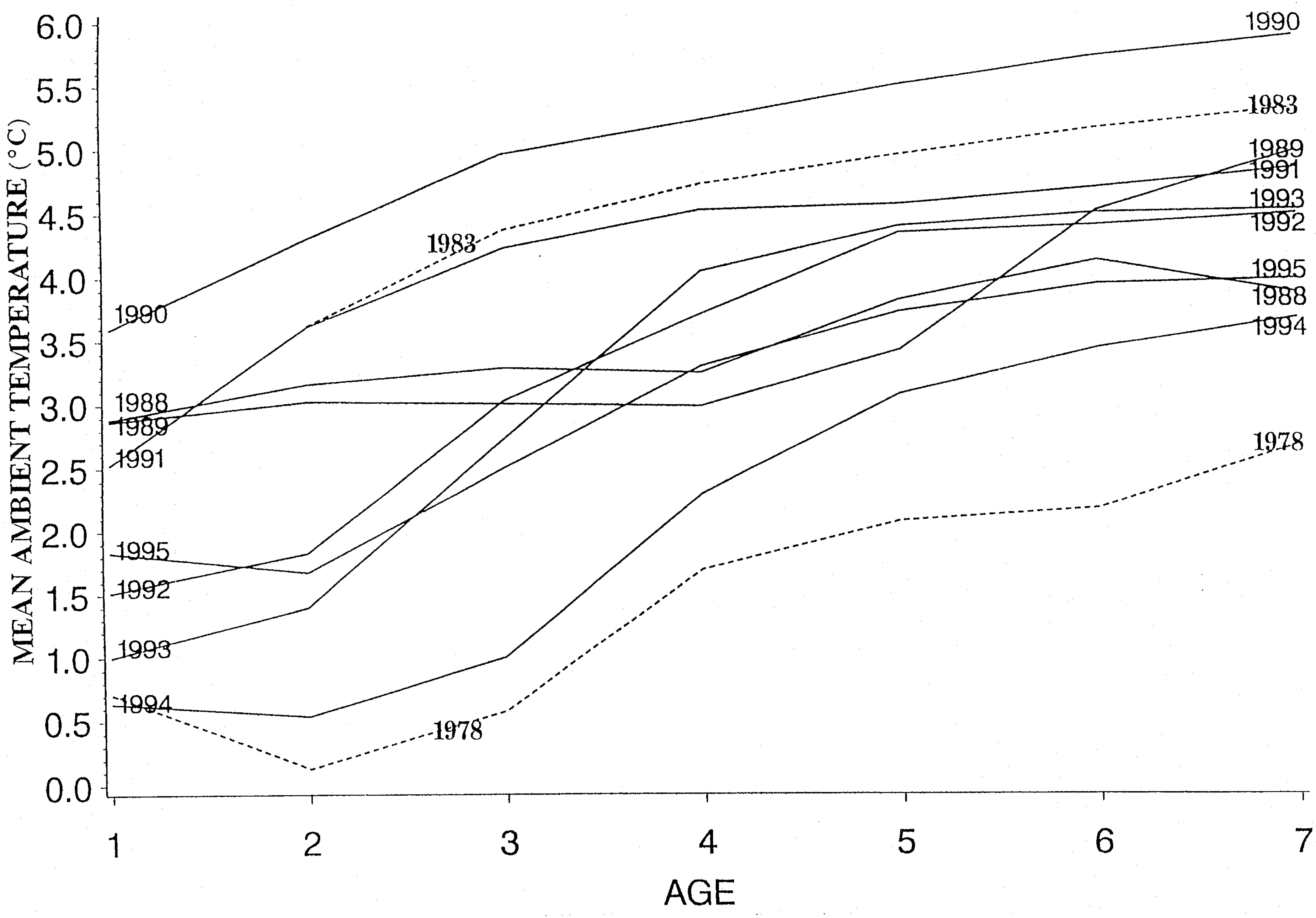


Figure 10. Mean ambient temperatures of Northeast Arctic cod by age for the years 1988-1995. The values from 1978 and 1983 (stippled lines) are the lowest and highest in Nakken and Raknes (1987).

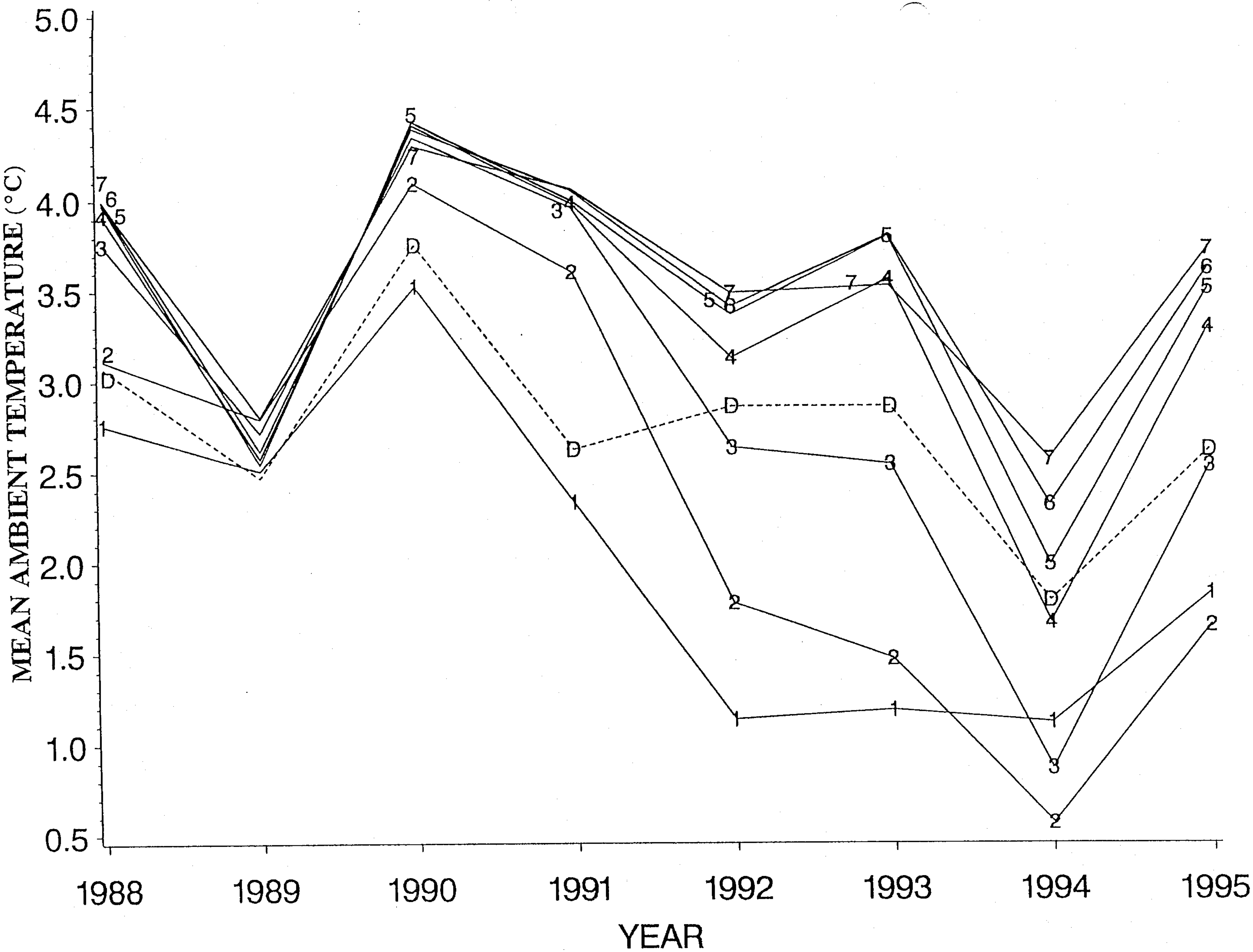


Figure 11. Mean ambient temperature by age groups 1-7 and mean bottom temperature (D) in subarea D.

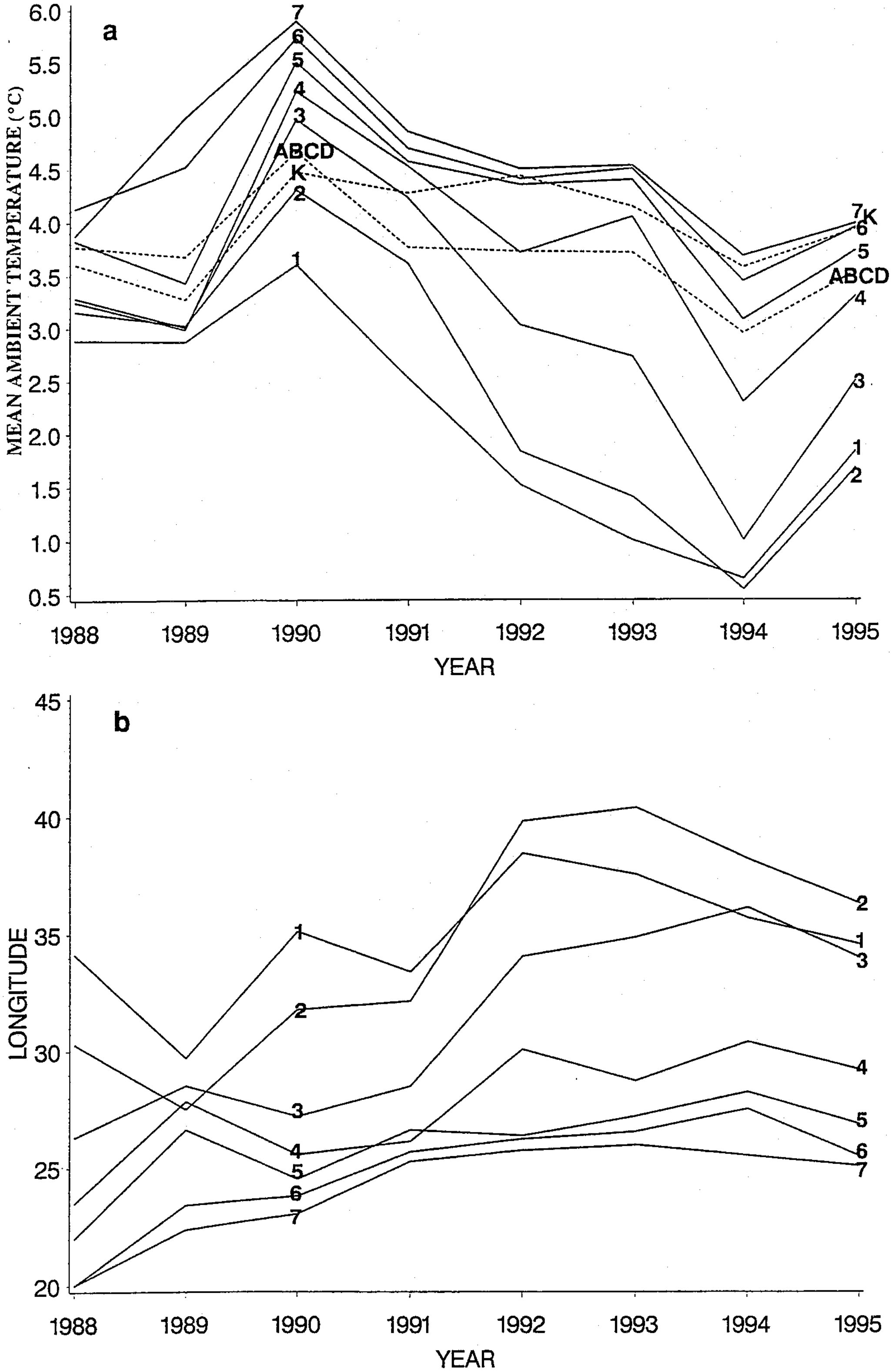


Figure 12. Mean ambient temperatures (a) and centres of mass of distribution (b, in degrees eastern longitude) of Northeast arctic cod 1988-1995 for agegroups 1 to 7. The mean bottom temperature in the ABCD area (ABCD) and the 0-200m December-February temperature mean from the Kola section (K) are shown (stippled lines).

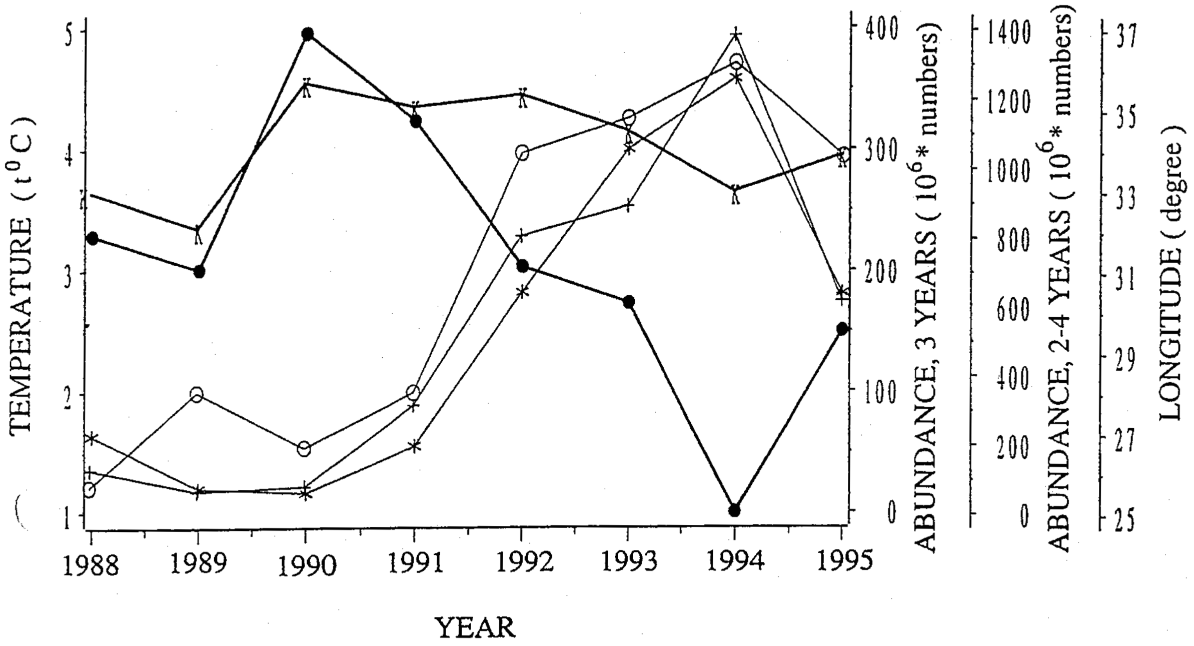


Figure 13. Location and abundance of 3 year old cod and temperatures in February 1988-1995. Abundance index (acoustic, from Korsbrekke *et al.* 1995) of 3 year (*) and 2-4 year old cod (+) as well as the longitude of the centre of mass of distribution for age group 3 (open circle) versus mean acoustic ambient temperature for 3 year old cod (filled circle) and mean temperature in the Kola section (K).

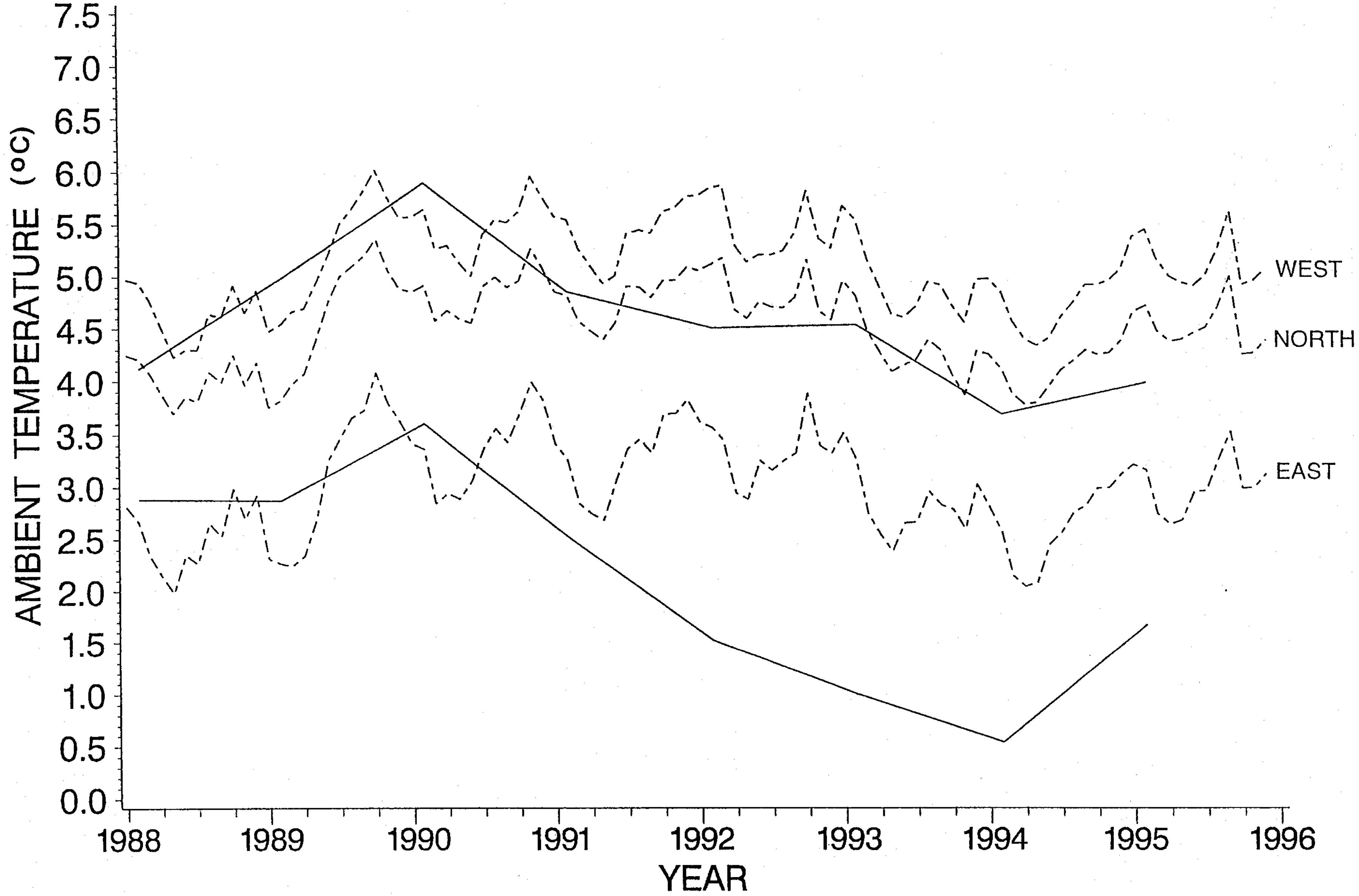


Figure 14. Ambient temperatures and temperatures used for estimation of consumption. Stippled lines show temperatures used by Bogstad and Mehl (in prep.) Full lines show upper and lower limits of mean ambient winter temperatures as estimated by us.