ICES Journal of Marine Science, 55: 67–85. 1998

Ambient temperature and distribution of north-east Arctic cod

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Ottersen, G., Michalsen, K., and Nakken, O. 1998. Ambient temperature and distribution of north-east Arctic cod. – ICES Journal of Marine Science, 55: 67–85.

Many studies on the effects of temperature on fish distribution and population parameters have considered the temperature and its variability at fixed stations or sections rather than the ambient temperature actually surrounding the fish. In the present paper ambient winter temperature was estimated for 1–7 year-old north-east Arctic cod in the period 1988–1995 from spatial distributions of fish density and temperature. Four different estimates were calculated for each age and year based on fish density observations from acoustic and bottom-trawl surveys and temperature recordings at the bottom, as well as averaged from 100 m depth to bottom. The estimates of ambient temperature were compared with each other and with temperature series in fixed areas and a standard section, the Kola meridian. The inter-annual variability in ambient winter temperature was found to be larger than in the Kola section series. Older fish were found at higher temperatures. For the younger age groups the range extended eastwards when numbers were high. This could explain the observed decrease of mean ambient temperatures in which cod were found during a relatively warm period in the Barents Sea. The mean ambient temperatures are also compared with the temperatures used for calculations of consumption rate by cod in the ICES Working groups.

Key words: cod, ambient temperature, distribution, Barents Sea.

Received 1 July 1996; accepted 5 March 1997.

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Introduction

Many studies relating to the effects of field temperatures on fish distribution and population parameters have considered the temperature and its variations at fixed locations rather than the ambient temperature, i.e. the temperature actually surrounding the fish. Since fish often inhabit regions of relatively large horizontal temperature gradients they may, depending on their movements, experience temperature variations that are quite different from those in any geographically fixed point.

For north-east Arctic cod in the Barents Sea and Svalbard waters (Fig. 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 (Woodhead and Woodhead, 1965; Mehl *et al.*, 1985). Cod are mainly found at depths below 100 m (Korsbrekke *et al.*, 1995) where seasonal variations at fixed locations are rather small, 1–3°C (Ottersen and Ådlandsvik, 1993). Consequently the majority of adults, 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 less extensive seasonal migration takes place for the immature fish, ages 3–6 years, which prey on capelin migrating towards the coast of Russia and northern Norway in winter–spring (Mehl *et al.*, 1985). Seasonal migrations of 1 and 2-year-old fish appear to be smaller. Cod of age 1 seem to remain in the areas where they settled during autumn as 0-group, at the end of their pelagic drift phase (Maslov, 1944, 1960; Baranenkova, 1957). In accordance with these seasonal movements through the temperature field one would expect that ambient temperatures of the various age groups of north-east Arctic cod are higher during winter–spring than summer–autumn. One would also expect that ambient winter temperatures are higher for older fish as demonstrated by Nakken and Raknes (1987) and Shevelev *et al.* (1987).

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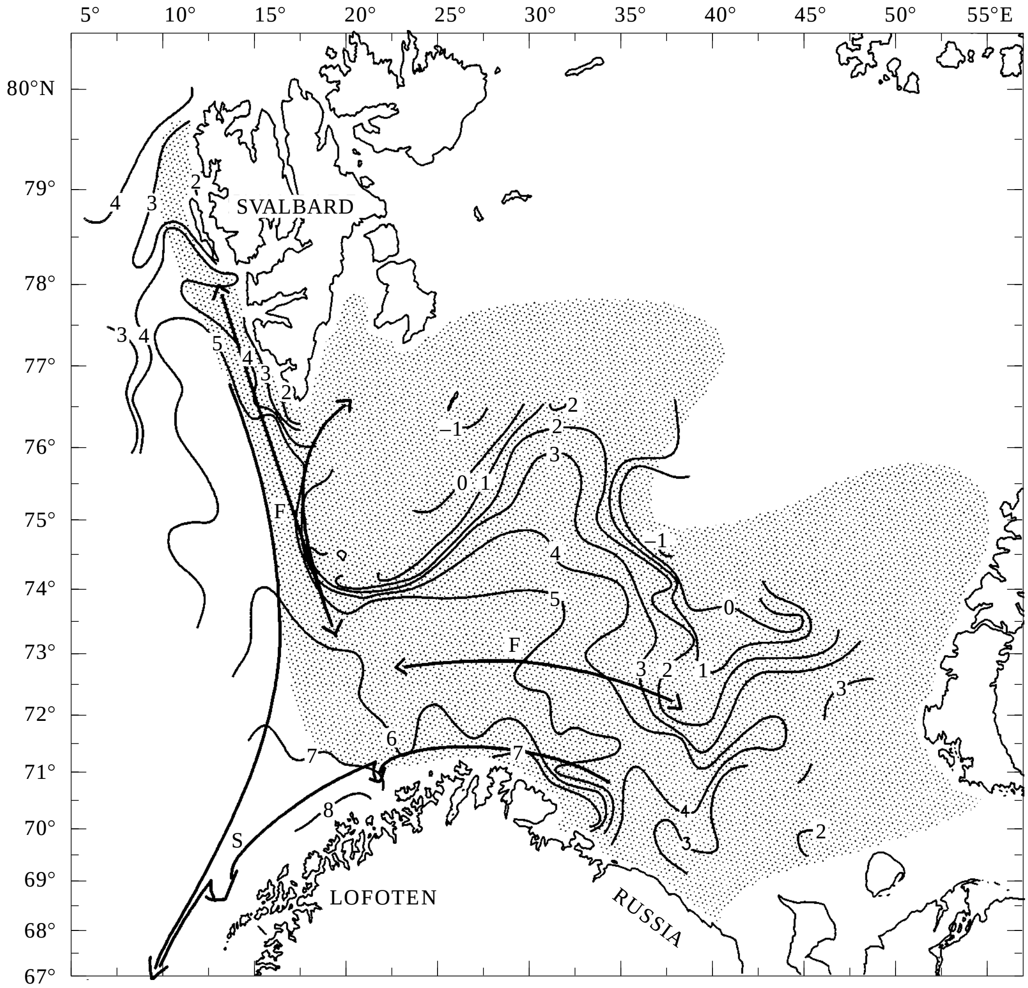

Figure 1. The area of distribution of north-east Arctic cod and isotherms (°C) at 100 m depth. Feeding areas (hatched), seasonal feeding migrations (F) and spawning migrations (S) are indicated (see Mehl, 1991). Temperature distribution is for August 1995 (ICES., 1996c).

In addition to these seasonal variations, temperature-related displacement of north-east Arctic cod has been reported on the inter-annual 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 is extended towards the east and north as compared to periods of cold climate when the fish tend to concentrate in the south-western part of the Barents Sea. Positive effects of higher temperatures on recruitment and growth have also been shown (see Nakken, 1994; Ottersen *et al.*, 1994; 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 annual consumption by cod of prey species, particularly capelin, and in predicting cod growth (ICES, 1996a, b). Due to lack of ambient temperatures, climatological temperatures (Ottersen and Ådlandsvik, 1993) at a few fixed points are used together with temperatures from the Kola section (Bochkov, 1982) which capture the temporal variability (Bogstad and Mehl, 1996).

Brander (1995) who examined 17 north Atlantic cod stocks including north-east Arctic cod 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

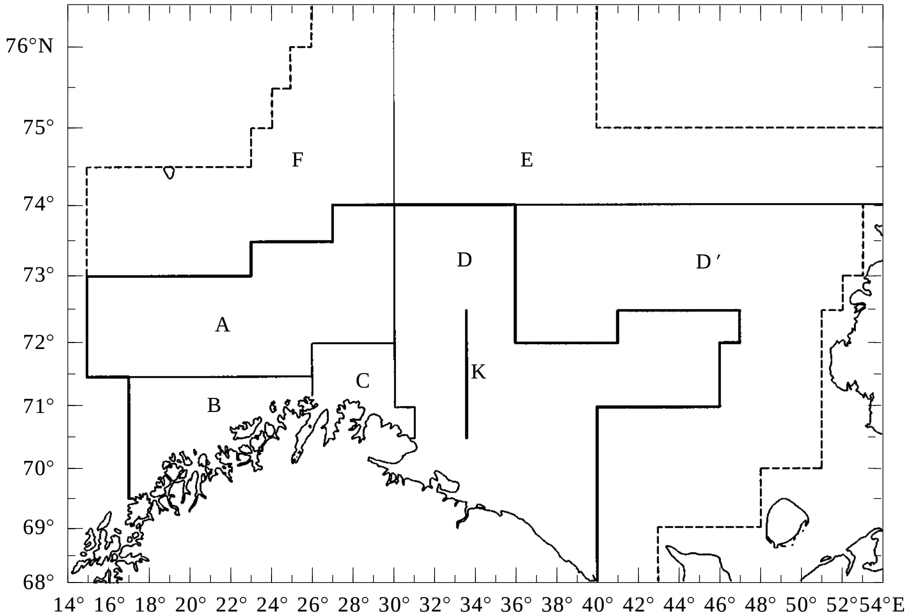

Figure 2. The survey area. Subareas for calculating indices of abundance and average temperature are framed. The Kola section (K) for which monthly temperature means have been established is also shown.

investigate the effect in detail for individual stocks, data on temperature and fish distribution need to be analysed jointly."

Nakken and Raknes (1987) calculated ambient temperature for north-east Arctic cod from horizontal distribution of bottom temperature and acoustic estimates of fish column densities (number per unit area). Their estimates were thus arrived at under the assumption that all cod were recorded close to the bottom. In the Barents Sea cod are often found in all depth layers below 100–150 m and thus up to 200 m above the bottom (Korsbrekke *et al.*, 1995). Geographical and temporal variations in such a vertical distribution pattern may bias the two types of density estimates that are available, acoustic and swept area, in opposite directions. In addition, during the late 1980s, and particularly the 1990s, both the overall area covered by the cruises and the station density increased. It was therefore felt that a more comprehensive study than that of Nakken and Raknes (1987) would be appropriate, utilizing both types of density estimates as well as vertically integrated temperatures in the calculations of ambient temperature.

The present work describes alternative methods of estimating ambient temperature for north-east Arctic cod. Variability in ambient temperature between different age groups and years is studied. We also assess how our results would affect the estimates of consumption by cod arrived at by the ICES Atlanto-Scandian Herring, Capelin and Blue Whiting Assessment Working Group (Bogstad and Mehl, 1996).

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. The surveys followed a stratified random design until 1990 and from 1991 onwards a stratified design. Until 1992 the area covered by the bottom trawling was limited to ABCD (Fig. 2), while the acoustic recordings covered a slightly larger area. While the number of stations trawled varied, the entire ABCD area was always reasonably well covered. Since 1993 bottom-trawling and acoustic data covered the same area, expanded to the north and east in order to provide better coverage of the geographical distribution of the younger age groups of cod. Acoustic and swept area abundance estimates and numbers-at-age are available for all years in ICES (1996a). During the cruises, CTD profiles were taken throughout the Barents Sea. The number of stations ranged between 148 (1989) and 389 (1995). Monthly 0–200 m depth sea temperature averages from the Russian hydrographical section off the Kola Peninsula (Bochkov, 1982; Fig. 2) are also used.

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

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

where ρ (x, y, z, t) is fish density at position (x, y, z) and time t, T (x, y, z, t) the corresponding temperature (see below), and the integration is done over the whole distribution volume of the fish and the year. In our case vertically interpolated fish density and temperature values are used and t is fixed to February, simplifying Equation (1). The ambient temperature calculated for this time is taken to be representative of the temperature conditions the cod have lived in throughout the winter. The two types of fish density estimates, acoustic and swept area, were separately combined with two temperature representations, at the bottom and the average in the 100 m depth-to-bottom layer, resulting in four estimates of ambient temperature. This was done separately for each age group and year. Procedures of data processing and analyses are given below.

Temperature

The CTD temperatures, from the database's vertical resolution of 5 m, were interpolated vertically to single horizontal fields in two ways. To represent the bottom temperature the average of the two deepest measurements from each station were used, while the average from 100 m depth to the bottom was taken to represent the temperature of the total vertical range inhabited by cod.

Separately, the bottom and 100 m depth-to-bottom temperature values were then interpolated horizontally to a (nearly) equidistant 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. Haltiner and Williams, 1980 or Smith, 1985). The interpolation scheme is explained by Taylor (1976) while the actual programs used are described by Ottersen (1991). Temperature values representative for each 30 min latitude times 1 degree longitude acoustical rectangle were calculated by averaging the values from the 20 times 20 km grid cells within the rectangle. Mean temperatures within each subarea (Fig. 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. Additional values for ABCD were calculated as averages of the means of each of the four regions weighted by the area of each region as given in Korsbrekke *et al.* (1995).

Swept area densities

In the bottom-trawl surveys a Campelen 1800 shrimp trawl was used. Further specifications on equipment and methods are given in Korsbrekke *et al.* (1995) and Aglen and Nakken (1997). Density estimates (number of fish per square nautical mile, ρ) were calculated for each 5 cm length group.

$$\rho = c/(ds) \quad (2)$$

where c is numbers at length in the catch; d is distance towed, i.e. length of swept area; and s is effective spread, i.e. width of swept area.

Equation 2 was applied haul-by-haul, densities from bottom trawl stations in predetermined positions as well as from catches taken for identification of acoustic scatters being computed. 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 (Fig. 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 (Aglen and Nakken, 1997), 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.

$$\rho = (s_A/\overline{\sigma}) \cdot p \quad (3)$$

where s_A is acoustic backscattering per unit area for cod, $\overline{\sigma}$ is the mean scattering cross-section of individual fish and p is the proportion of fish in the length group from swept area estimates.

Equation (3) was applied for rectangles of 30 minutes latitude and 1 degree longitude, from surface to the bottom, using mean values of s_A, $\overline{\sigma}$ and p as input. Estimated density-at-length was converted to absolute numbers-at-length by multiplying by the area of the rectangle. As for the swept area estimates, numbers-at-length were 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.

$$\overline{\mathrm{lon}}=\Sigma(\mathrm{N(x, y)} \cdot \mathrm{lon(x, y)})/\Sigma\mathrm{N(x, y)}, \text{ and} \qquad (4)$$

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

Ambient temperature estimates

Ambient temperature values relevant to acoustic density estimates were worked out from the temperature values for the appropriate rectangles. Mean ambient temperatures were determined separately for each age group and year from Equation (1), in practice by dividing the sum of the products of number of fish and temperature over all rectangles by the sum of number of fish:

$$\overline{\mathrm{T_{amb}}}=\Sigma(\mathrm{N(x, y)} \cdot \mathrm{T(x, y)})/\Sigma\mathrm{N(x, y)}. \qquad (5)$$

Relative frequency distributions within temperature intervals were calculated separately for each age group and year by summing the number of 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 (1) in the following manner: each trawl station was first given the temperature value of the 20 times 20 km cell in which it is situated. Mean ambient temperatures for each age group and year were then worked out as

$$\overline{\mathrm{T_{amb}}}=\left(\sum_{\mathrm{int}<-1}^{\mathrm{int}\geq 7} \mathrm{N_{int}} \cdot \mathrm{T_{int}}\right)/\sum_{\mathrm{int}<-1}^{\mathrm{int}\geq 7} \mathrm{N_{int}} \qquad (6)$$

where $\mathrm{N_{int}}=\mathrm{Area_{int}} \cdot \overline{\rho}_{\mathrm{int}}$, 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. $\mathrm{T_{int}}$ is the midpoint in each interval ranging from -1.25°C to 7.25°C. Relative frequency distributions for each age group and year were in this case worked out within each temperature interval by dividing $\mathrm{N_{int}}$ by the total number of fish.

Linear regression analyses between different ambient and mean temperatures, with and without allowing for an intercept, were performed separately for each age group 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. 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 compute the different ambient and mean temperatures separately for each age group. While an ordinary t-test would have tested for differences in temporally averaged ambient temperatures, the paired test examines if, on average, the difference within single years is different from zero. The significance levels should be regarded as approximate, due to the assumptions of normality and indpendence not being fulfilled for all cases.

Results

Temperature and its variation in space and time

Inter-annual variation of winter bottom temperature during the 1988–1995 period is shown in Figure 3 for the subareas given in Figure 2 and the Kola section. In Table 1 means of the differences in temperature between the 100 m depth to bottom and bottom values are given. 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, i.e. D, A, C, B, with the difference between B and D varying from 2.60 deg C in 1990 to 3.61 deg C in 1991. The simple averages for ABCD are consistently above the weighted values while the variability patterns are similar, as is the Kola section temperature variability (Fig. 3). The level of temperature in the section is in best agreement with that in subarea A, not with subarea D where it is situated. As seen by the temperature differences in Table 1 the 100 m depth-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.

Fish density and its variation in space and time

In order to visualize the horizontal distribution of fish density and temperature for each year, annual maps of distributions of echo density (all sizes) and swept area densities (fish bigger than 30 cm) were studied together with bottom temperatures. The two sets of maps showed 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. Maps of 1990 and 1994 are shown in Figure 4. Centres of mass of distribution for each age group were calculated from each year's acoustic density distribution. Curves enveloping the eight centres of mass of each age group are shown in Figure 5. Older age groups were distributed further west than the younger ones. Figure 5 also shows that older fish have smaller inter-annual variation in the distribution centres of mass than younger fish.

Figure 6 shows systematic differences in vertical distribution of cod among years. There was a tendency for

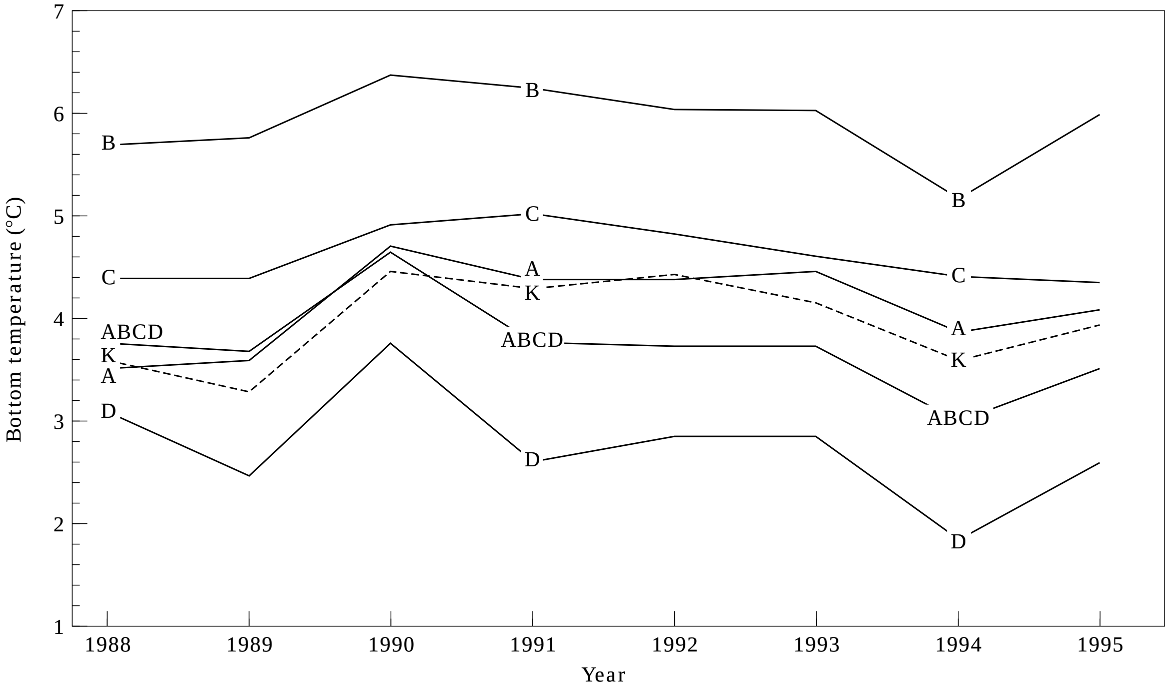

Figure 3. Average bottom temperature (°C), in February 1988–1995 in subareas A, B, C and D, in ABCD as a whole and in the Kola section (K).

Table 1. Temperature differences, Diff, defined as temperature 100 m to bottom minus the bottom 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. Differences between additional means for the ABCD area calculated by weighting the means from each of A, B, C and D by their area are also given (ABCD-WGT). N denotes the number of $\frac{1}{2}$ degree latitude times 1 degree longitude acoustical rectangles covered. Areas with no or insufficient coverage are noted —.

Year	1988		1989		1990		1991		1992		1993		1994		1995	
Region	N	Diff	N	Diff	N	Diff	N	Diff	N	Diff	N	Diff	N	Diff	N	Diff
Total	142	0.47	149	0.49	109	0.16	191	0.51	181	0.38	271	0.44	282	0.53	295	0.49
ABCD	124	0.35	127	0.41	108	0.16	161	0.41	167	0.37	165	0.33	168	0.34	167	0.39
ABCD-WGT	124	0.25	127	0.40	108	0.14	161	0.43	167	0.36	165	0.33	168	0.35	167	0.39
A	53	0.65	49	0.72	37	0.54	49	0.66	48	0.37	47	0.57	49	0.44	48	0.61
B	18	0.11	22	0.04	18	− 0.18	19	− 0.10	16	− 0.08	15	− 0.05	19	− 0.04	18	− 0.04
C	13	0.24	13	0.16	14	− 0.01	12	0.05	11	0.24	11	0.48	11	0.05	12	0.61
D	40	0.08	43	0.32	39	0.01	81	0.44	92	0.46	92	0.26	89	0.40	89	0.33
D′	—	—	—	—	—	—	—	—	—	—	48	0.61	47	0.55	50	0.31
E	—	—	—	—	—	—	—	—	—	—	19	0.48	25	0.70	29	0.53
F	16	1.49	22	0.95	—	—	29	1.07	—	—	42	0.65	42	1.17	51	0.98

an increasing proportion of fish to be close to the bottom from 1993 to 1995. In 1993 about 43 and 73% of the total acoustic recordings of cod were obtained at distances respectively less than 50 and 100 m from the bottom, the 1995 percentages were 65 and 90.

Ambient temperature and its variation

In Table 2 the relative frequency distribution of number of fish estimated from acoustic density is shown by age and bottom temperature. Two systematic patterns, which also show up in the corresponding frequency distribution based on swept area density, should be noted. Each year the distribution density indicated that older fish were found in warmer water than younger fish. In some years, e.g. 1994, the whole density distribution was shifted towards lower temperatures, in other years, e.g. 1990, towards higher temperatures. Focusing on acoustic estimates of 3-year-old cod, the median bottom temperature in 1994 was in the 0.5 to 1°C interval, in

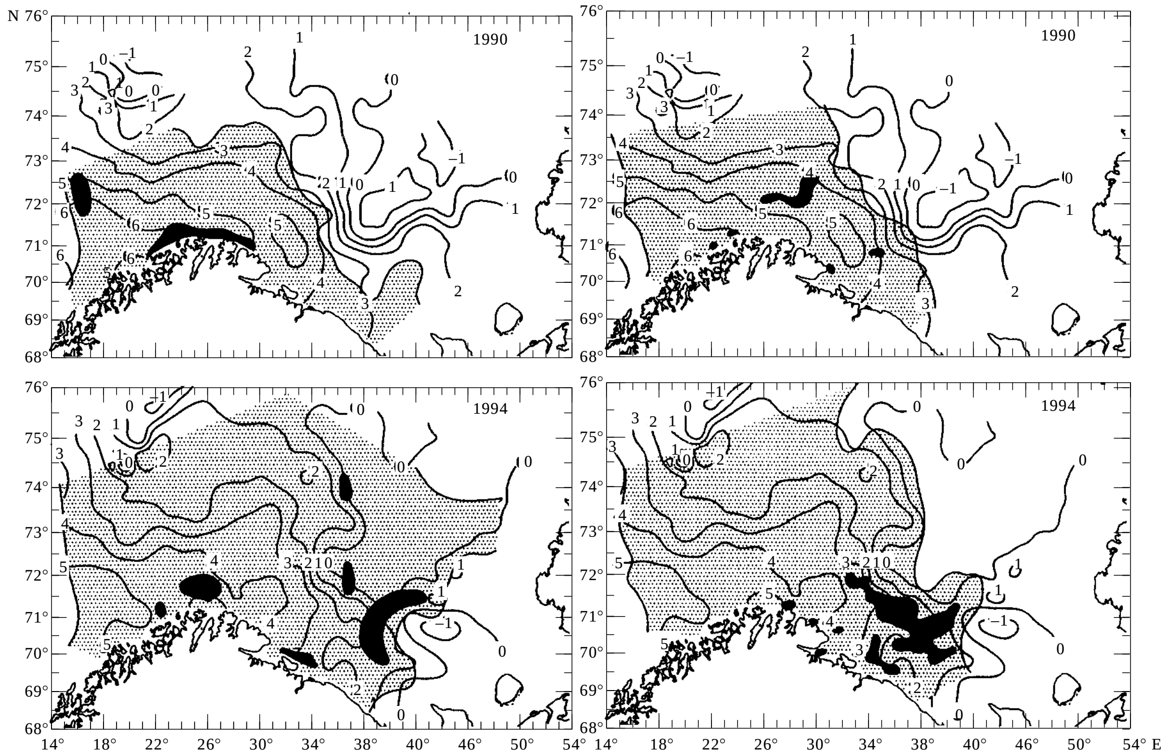

Figure 4. Distribution of cod density (shaded areas) and bottom temperature (isotherms, °C) in February 1990 (upper graph) and 1994 (lower graph). The left graphs show echo densities (back scattering coefficient, s_A) of all cod. Dark shading for s_A>100 m^2 (nautical mile)$^{-2}$. The right graphs show swept area densities (p) of cod >30 cm in length. Dark shading for p>10 000 specimens (nautical mile)$^{-2}$.

1990 in the interval from 4.5 to 5°C. Mean ambient winter temperatures, both those estimated by acoustic density (Table 2) and those calculated from swept area densities, show large inter-annual differences. Figure 7, which shows mean ambient temperatures calculated from acoustic estimates and bottom temperature, visualizes the increase with age found in Table 2.

A systematic study of the different estimates of ambient temperature was done by regression analyses and tests (Table 3). The mean 100 m depth-to-bottom ambient temperatures were found to be higher than those at the bottom for all ages, acoustic and swept area estimates. The mean ambient temperatures based on acoustical estimates were higher (equal in one case) than the swept area estimates at all ages and both vertical temperature levels. The differences were, however, small and not statistically significant for fish of age 1, 2 and (marginally) 3. Mean ambient winter temperatures for cod of ages 1, 2 and 3 were significantly lower than the corresponding Kola section temperature (Table 3). For ages 4 and 5 the differences between ambient and Kola temperature means were not statistically significant, while the ambient temperatures of 6 and 7-year-old cod were higher than the Kola section temperature. The same pattern was reflected in the slope parameters and root mean-square errors of the regression analyses. A similar situation was found when comparing ambient temperatures with mean bottom temperature within the ABCD region (Fig. 2).

The temporal development of the four different ambient temperature representations are shown in Figure 8 for 3 and 5-year-old cod together with series of mean temperature from three geographically fixed positions. Figure 8 (upper graph) shows how the three mean temperatures over-estimate the ambient temperatures of cod at age 3 in recent years while Figure 8 (lower graph) indicates that the correspondence is better with the ambient temperature for 5-year-old fish. Table 3 and Figure 8 further show that the inter-annual variability in ambient temperatures is higher than that reflected in temperatures at geographically fixed areas.

Our results gave no clear indication of any single method of calculation of ambient temperature giving better estimates than the other three. To allow for comparison with the values of Nakken and Raknes (1987) ambient temperature based on bottom

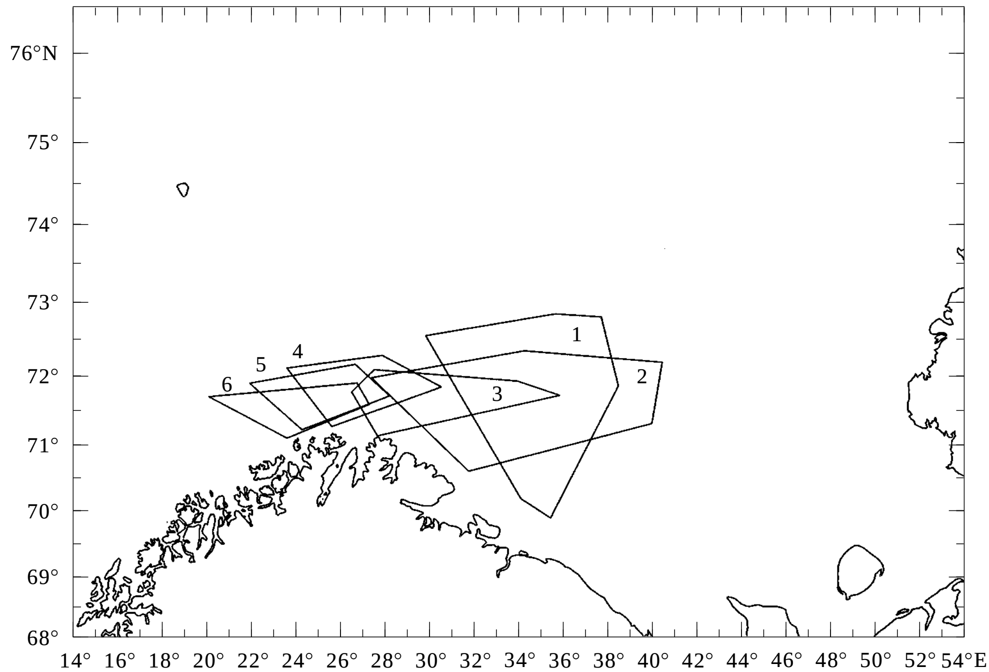

Figure 5. Areas within which the centre of mass of distribution of each age group (1–6 years) were located February 1988–1995.

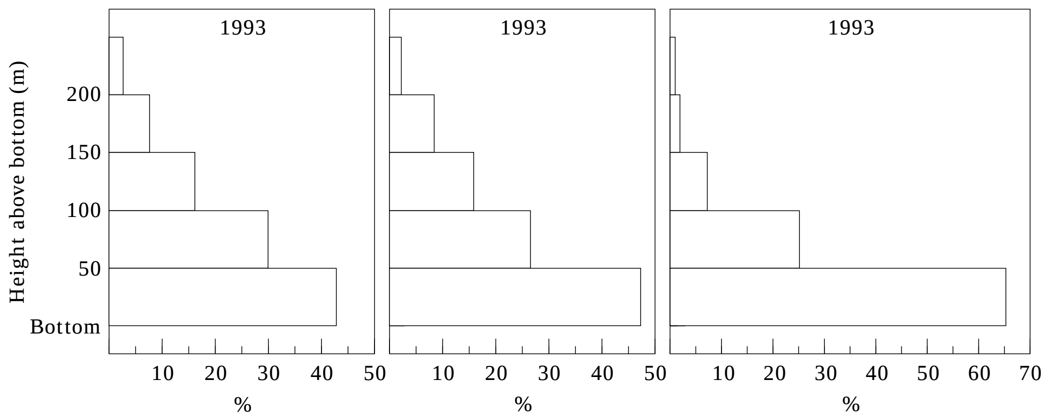

Figure 6. The vertical distribution of cod relative to the bottom in February 1993–1995. Horizontally accumulated s_A-values in 50 m height intervals given as percent of total (from Korsbrekke *et al.*, 1995).

temperature and acoustic estimates was chosen for the rest of this paper. Figure 9 (upper graph) shows that the years 1992–1995, as well as 1978, had particularly low ambient temperatures for cod of age 3 relative to those of the Kola section. Inter-annual variability in ambient temperature for age groups 3 and 5 was also shown to be a lot higher than reflected in the Kola section temperature. 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°C, a range of 1.7 deg C, while the ambient temperature for 3-year-old cod varied from 0.6 to 5.0°C, a range of 4.4 deg C. For other ages the range in ambient temperature was typically somewhat smaller but not below 3.5 deg C, still more than twice that of the Kola section.

Comparison of fish distribution patterns and temperature

Figure 10 shows the development of ambient temperatures (upper graph) and the location of the fish as

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, $\overline{T}_b$, or temperature in the 100 m depth-to-bottom layer, $\overline{T}_p$.

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

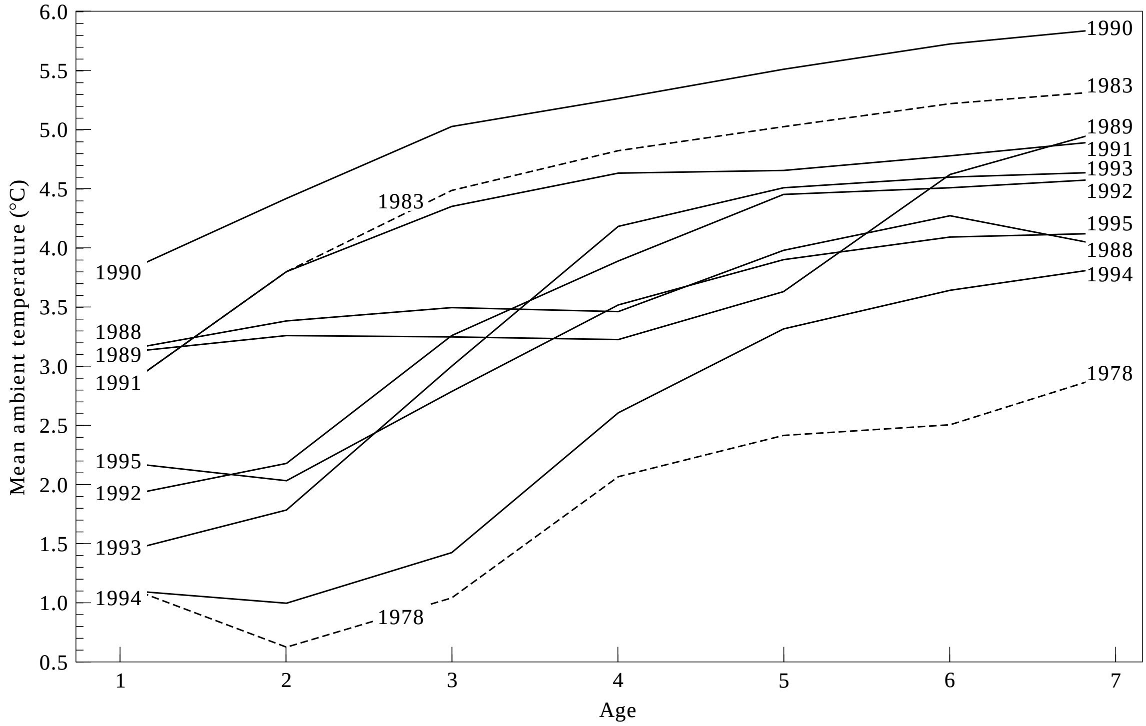

Figure 7. Mean ambient temperatures of north-east Arctic cod by age for the years 1988–1995. The values from 1978 and 1983 (stippled lines) are the lowest and highest in Nakken and Raknes (1987).

represented by the longitude of the centre of mass of distribution (lower graph) 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, coincided with a decrease in mean ambient temperature. From 1993 to 1994 the temperature in the Kola section as well as the mean for the ABCD area decreased, while the mass centre of fish aged 3–6 continued to shift further eastwards.

From 1993–1995 the distribution of the two youngest age groups again showed a somewhat different pattern from 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. It also appears that the longitudinal location of the 1, 2 and 3-year-old cod gradually became more similar from 1992 to 1995 and that the 2-year-old fish in these years were located slightly further east than the 1-year olds. The low ambient temperatures experienced by the older age groups in 1994 seem to have led to a more westerly distribution the year after.

Figure 11 shows that for 3-year-old cod the increasingly eastward location from 1990 to 1994 coincided not only with a decrease in the ambient temperature of this age group, but also with an increase in abundance.

Effects of 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. (ICES, 1996a) as described by Bogstad and Gjøsæter (1994) and Bogstad and Mehl (1996). The temperatures used in these calculations are monthly climatological temperatures (Ottersen and Ådlandsvik, 1993) in three fixed locations that are regarded as representative for the western, eastern and northern parts of the distribution area of the fish. The inter-annual 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, 1996). Consumption by age group is thus estimated for each of the three areas and total consumption is found by summation.

Figure 12 indicates the ambient temperatures estimated by the procedure described above as well as the range of ambient temperature as estimated by us. Both the inter-annual variability in mean ambient winter

Table 3. 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, 100 m 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, 100 m bottom/ trawl, 100 m 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
Acoustic, bottom/ trawl, 100 m 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 December–February	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

temperature of each age group and the variation between age groups is larger in our estimates. For the period 1992–1995 the mean ambient winter temperature of ages 1–3 years were 1–3 deg C lower than those used in the consumption estimates, a difference that would generate an upward error of 10–30% in the consumption estimates (Bogstad and Gjøsæter, 1994).

Discussion

Our results indicate that inter-annual temperature variability in the Barents Sea is mainly of large scale origin, in synchrony throughout the different areas (Fig. 3). The Kola section temperature has been used as an indicator of the general Barents Sea temperature situation by

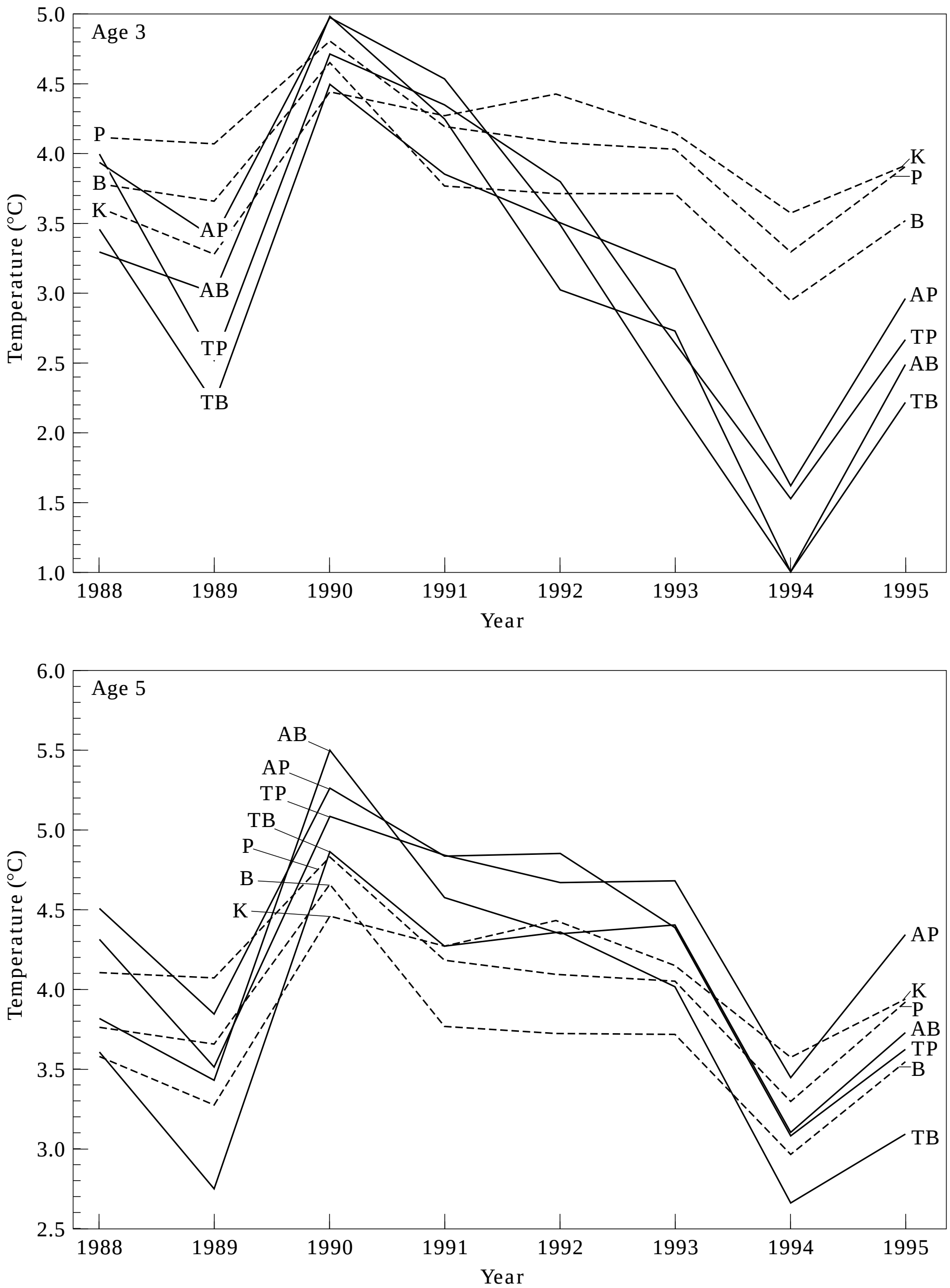

Figure 8. Mean ambient temperatures of 3-year-old cod (upper graph) and 5-year-old cod (lower graph) in February 1988–1995 based on acoustic estimates and temperatures 100 m bottom (AP), trawl estimates and temperatures 100 m bottom (TP), acoustic estimates and bottom temperatures (AB) and trawl estimates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

several authors, e.g. Borisov and Elizarov (1989) and Ottersen and Sundby (1995). That the temperature in the section is in best agreement with that in subarea A, not with subarea D where it is situated, is not unreasonable. The Kola section is situated in the western part of D (Fig. 2) where the Atlantic water masses are the dominating influence, as they are also further west. The average temperature in the large area D is significantly lower due to the colder water in the eastern parts. The slightly higher bottom temperature than vertical average from 100 m depth to bottom, peculiar to area B can be explained by the convection process connected to the

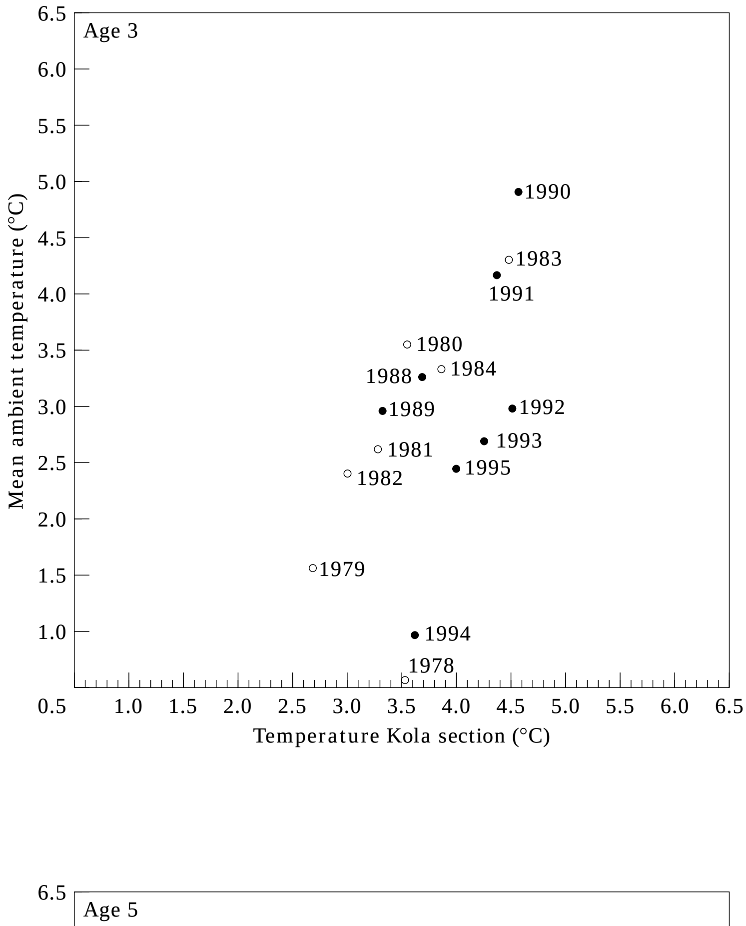

Figure 9. Mean ambient temperatures of 3-year-old cod (upper graph) and 5-year-old cod (lower graph) plotted against mean temperatures in the Kola section. Years 1978–1984, shown with smaller, open circles and thin font, are from Nakken and Raknes (1987). Note that the horizontal and vertical axes are equally scaled.

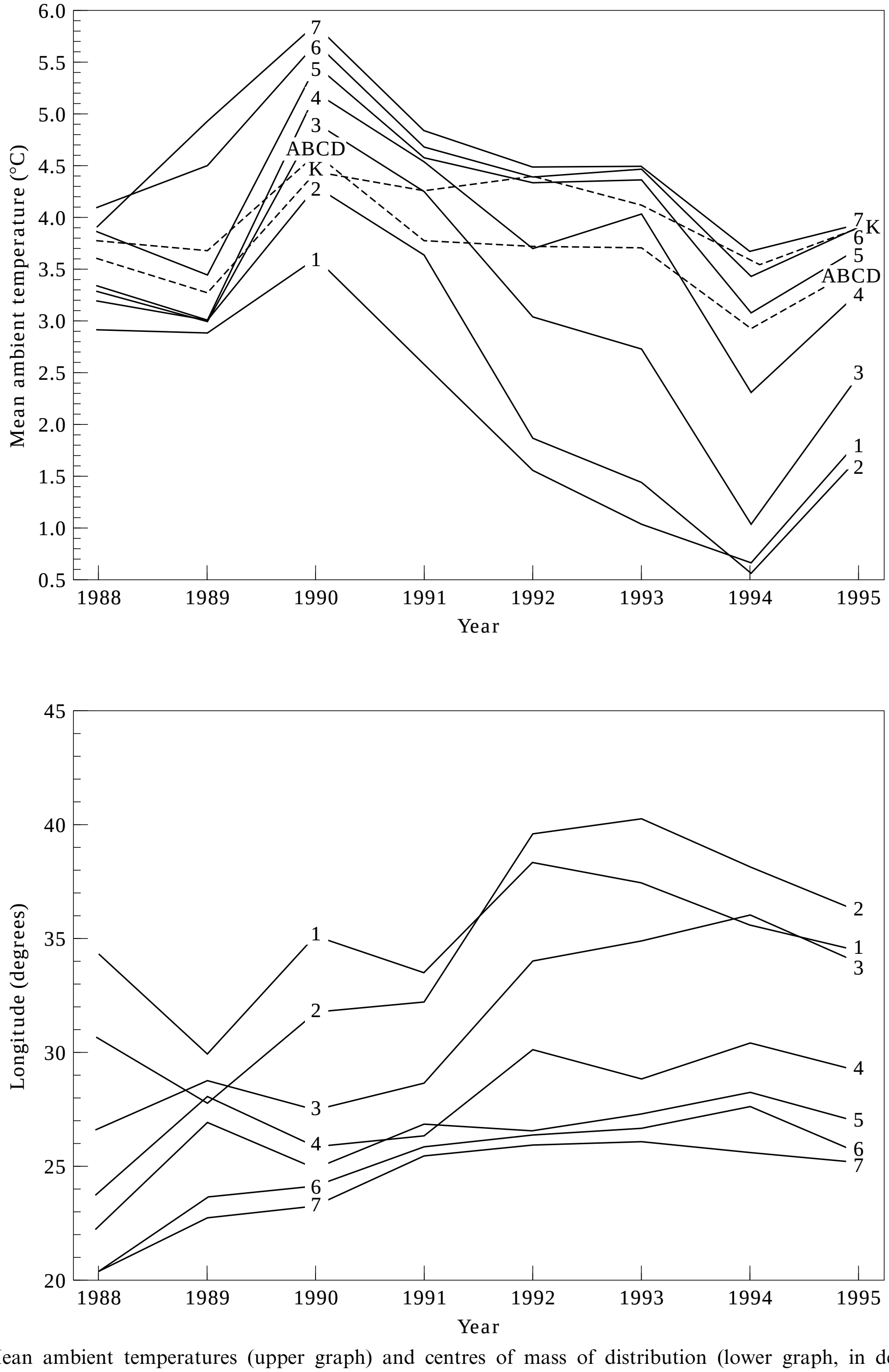

Figure 10. Mean ambient temperatures (upper graph) and centres of mass of distribution (lower graph, in degrees eastern longitude) of north-east Arctic cod 1988–1995 for age groups 1 to 7. The mean bottom temperature in the ABCD area (ABCD) and the 0–200 m December–February temperature mean from the Kola section (K) are also shown (stippled lines).

winter cooling of the ocean by the atmosphere not reaching the bottom layer in this area. For an extensive description of Barents Sea oceanography see Midttun (1989, 1990).

The four different estimates of ambient temperature of cod show a reasonable correlation (Fig. 8, Table 3), but there are differences that have to be explained. It is natural that the higher temperatures of the 100 m

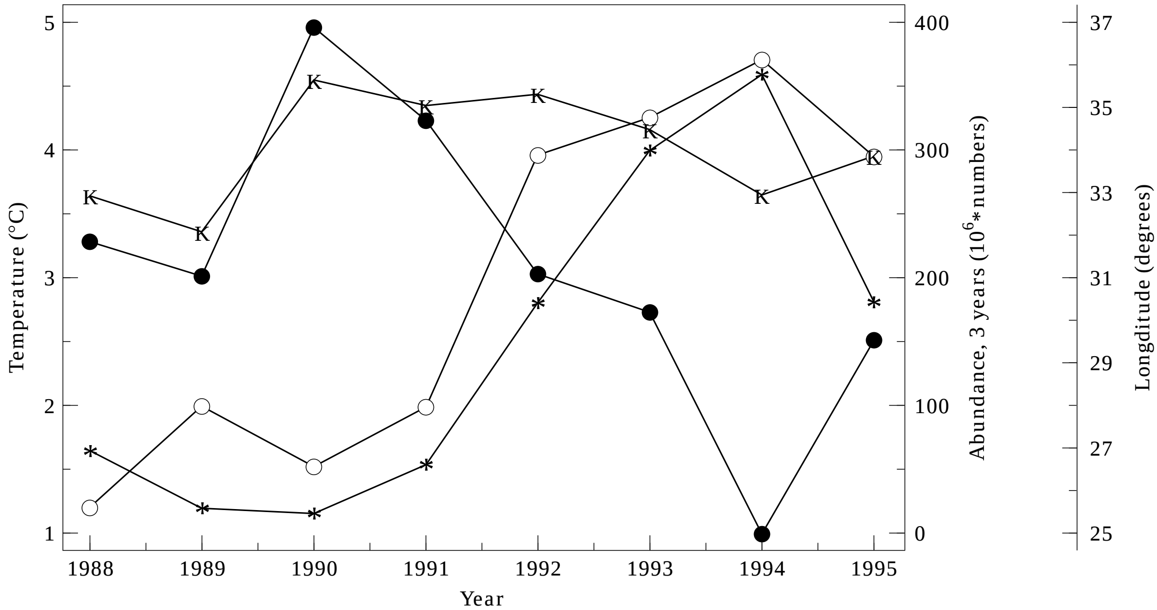

Figure 11. Location and abundance of 3-year-old cod and temperatures in February 1988–1995. Abundance index (acoustic, from Korsbrekke *et al.*, 1995) of 3-year-old cod (*), longitude of the centre of mass of distribution for age group 3 (open circle), (acoustic) mean ambient temperature for 3-year-old cod (filled circle) and mean temperature in the Kola section (K).

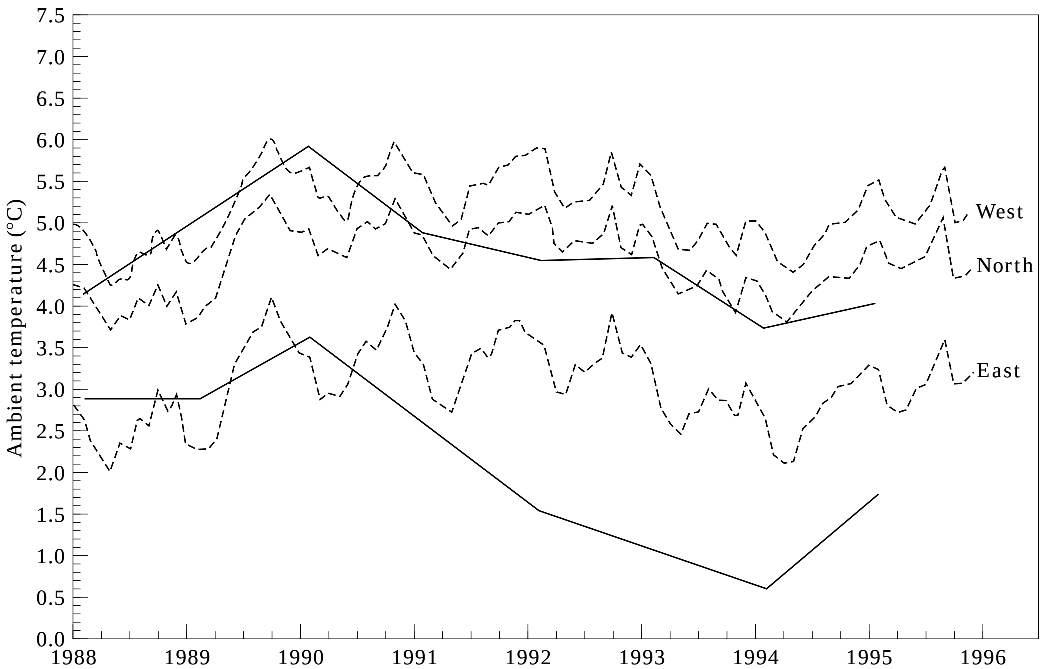

Figure 12. Ambient temperatures and temperatures used for estimation of consumption. Stippled lines show temperatures used by Bogstad and Mehl (1996). Full lines show upper and lower limits of mean ambient winter temperatures as estimated in the present paper.

depth-to-bottom interval, as compared in bottom temperature, found in most areas, must lead to the corresponding ambient temperature estimates being higher. The difference between acoustic and trawl-based ambient temperatures are more complicated, but two main factors can be identified with the former believed to be dominating; there are differences in fish density estimates and the manner of ambient temperature calculation. The temperature fields introduce no difference since they are identical.

Regarding the areas of higher fish densities, the echo and swept area densities (Fig. 4) show dissimilarities that to a large extent reflect differences in availability of fish to the sampling methods (Aglen and Nakken, 1997). Fish distributed close to or at the bottom are well within reach of the bottom trawl but less detectable by 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.

The swept area densities may also be effected by temperature-dependent capture efficiency. For a range in temperature from − 1 to 6°C as observed in Fig. 4 the capture efficiency will be affected in two ways (He, 1993). 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. In the upper range, 4–6°C, large cod are capable of maintaining swimming speeds of more than 3 knots for longer than 30 min, the duration of a trawl haul. These mechanisms imply that the temperature and size-dependent endurance swimming ability of cod should bias the swept area estimates downwards for small fish in the cold eastern parts of the Barents Sea and for large fish in the warmer south-western parts. However, the selection of large fish is questioned by Godø *et al.* (1990). They state that fish greater than 50 cm will also get caught due to what they call "catching by surprise". Since swept area densities are used in the calculation of proportions of number of fish at length, p (Equation (3)) for acoustic density estimates, the two sampling estimates should, at least, be comparable for number-at-age.

No clear conclusion regarding choice of ambient temperature representation could be drawn from this. Actually, Fig. 6 shows that the vertical distribution of the fish varies inter-annually, implying that the sampling methods and vertical temperature representations that are most suitable also differ between years.

Nakken and Raknes (1987), who studied the years 1978–1984, concluded that age groups 3 or older maintained their relative distribution within the temperature field more or less independently of the absolute values of temperature. Our results (Table 2, Fig. 7) show that this rule is also valid for 1988–1995 and indicate that 2-year-old cod also fit the pattern. Nakken and Raknes (1987) further 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, while the 1978 data were found to fit poorly to the trend. Figure 9 shows that not only in 1978, but also in 1992–1995 the ambient temperatures of cod at age 3, relative to those of the Kola section, were lower than in other years. The more significant decrease in the ambient temperature of this age group in recent years, compared with that observed in geographically fixed locations, can be related to an eastward shift in the distribution of 3-year-old cod during a period of high temperature in the Barents Sea. While the relation established by Nakken and Raknes (1987) no longer seems to hold for 3-year-old fish, Figure 9 (lower graph) indicates that the Kola section temperatures correlate better with the ambient temperature for 5-year-old fish, the only odd year out still being 1978.

The oustandingly high ambient temperatures for all age groups in 1990 (Fig. 7) can partly 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 (Fig. 4). 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 south-west (Midttun *et al.*, 1981), and older cod dominated the stock due to several years with weak recruitment (ICES, 1996b).

In addition to the factors above, the downward trend found in mean ambient temperature of all age groups, but particularly 1–3-year-old fish, following the 1990 maximum (Fig. 10) can to some degree be explained by the survey coverage until 1992 being restricted to the ABCD area (Fig. 2). This is expected to have led to the ambient temperatures of the younger, most easterly distributed, age groups being somewhat overestimated prior to 1993, particularly in the warm years of 1990–1992. In those years fish of age 3 and younger were recorded and caught at the eastern boundary of ABCD while fish east of the standard area in colder waters were not included in the estimates. This could also have influenced the calculations of centre of mass for these age groups and years so that the estimated longitudes might be too low.

All ambient temperatures used here have been for the winter, mainly February, but what is the connection between them and annual ambient temperatures? As mentioned in the introduction, the seasonal migrations of cod increase in range with age. The fish will be at their south- and western-most location in March–May and at their north- and eastern-most 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 (Fig. 1). It further implies that the seasonal variation in ambient temperature is mainly determined by how the fish move and to a lesser extent by the rather limited seasonal temperature variation in fixed points. Consequently, during the annual cycle, cod experience higher temperatures in March–May and lower in September–October as indicated by Jørgensen (1992). 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, which usually inhabits the waters to the north of the western part of our area of investigation (Figs 1 and 2) and makes up about 10–40% of the total abundance, varying from year class to year class (Aglen and Nakken, 1997). In this area there is a southward (winter) and northward (summer) migration (Fig. 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 will be inside our area of investigation in February, particularly from 1993 when the area was extended. For fish of ages 4–7 which undertake long 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% of the total abundance were not included in the present investigations.

Our finding for each of the years 1988–1995 that older age groups are on average distributed further west than younger (Fig. 5) supports results for earlier periods by Nakken and Raknes (1987) and Shevelev *et al.* (1987). The connection between high temperature and a northward and eastward extension of the habitat of north-east Arctic cod of all age groups has been established in earlier studies (Eggvin, 1938; Konstantinov, 1967, 1969; Nakken and Raknes, 1984). However, the distribution of a year class of cod could possibly also be influenced 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, 1960) found that 1-year-old cod remained close to where they settled on the bottom 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 10 (lower graph) does, however, not give any strong support or evidence for this scheme, the connection between the distributions at age 1 and 2 and that of 3-year-old cod generally being weak.

Nevertheless, from Figure 10 (lower graph) it appears that the longitudinal location of the 1–3-year-old cod gradually became more similar from 1992 to 1995. The results also indicate that 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 ICES (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 further east. Cannibalism may thus have counteracted a more westerly distribution with age of 1 to 3-year-old fish of the year classes 1991 to 1993.

The detected eastward displacement of 3-year-old cod during the relative warm period in the Barents Sea 1990–1994 coincided with low mean ambient temperatures (Fig. 10) as well as an increase in abundance of the age group (Fig. 11). From 1993 to 1994 the temperature in the Barents Sea decreased and one should expect that the fish would be distributed further westward in 1994 than in previous years, but instead the centre of mass 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. Figure 11 indicates that at high abundances the fish may extend their distribution towards the east, thus shifting the centre of mass of distribution eastwards, apparently independently 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 more slowly 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 ways in which the geographical distribution of a fish population might change in response to changes in overall population size. The patterns identified were; (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 north-east 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.

While our results clearly indicate a connection between east–west displacements of north-east Arctic cod and the varying water temperature in the Barents Sea, the mechanisms involved may be several. The results of this work show the importance of using some kind of ambient temperature representation when dealing with the connections between temperature and fish distribution. However, our study also indicates that careful consideration of the methods of calculation is necessary. Further study is required to determine whether changes in distributional pattern can be regarded as a response to temperature directly, to abundance, or to other temperature-related environmental factors (abiotic and biotic), e.g. temperature-induced changes in distribution of prey organisms as hypothesized by Shevelev *et al.* (1987).

Acknowledgements

The authors wish to thank Åge Fotland, Svein Lygren, Hildegunn Mjanger and Lisbeth Solbakken for help with the data and some of the figures. The work was financially supported by the Norwegian Research Council (NFR) and the Institute of Marine Research (IMR).

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