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GROWTH OF THE BARENTS SEA CAPELIN
COMPARED TO STOCK SIZE AND GEOGRAPHICAL DISTRIBUTION

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ABSTRACT

The growth of individual capelin in the Barents Sea stock was analysed
in relation to the geographical distribution and size of the stock in
the feeding season, and the density of fish in the feeding area. The
growth in the current feeding season was estimated using a model of
back-calculation of fish lengths from otolith zone widths. Stock size
and fish density were estimated using bioacoustical methods. A strong
correlation between the growth and the feeding area was found, while
no dependence between growth and stock size or fish density could be
demonstrated.

1. INTRODUCTION

The growth of individual capelin in the Barents Sea stock has been observed to vary substansially during the last 15 years. In the same period the stock size has also changed considerably. Up to 1980, the growth was found to be highest when the abundance was low and vice versa, and this observation naturally led to the assumption that the growth was density dependent and was hampered by scarsity of food due to high densities of fish. However, the feeding area for this stock has also changed during the same period, and so the growth variation could also possibly be explained by this shift in feeding area, either as a stand-alone effect or combined with a density dependent effect.

The geographical distribution, the growth, and the stock size, have changed in the following manner: In the first part of the seventies the stock was very large, had a northeasterly distribution in the feeding season, and had a slow growth of individuals. In the last part of the seventies and until 1982 the stock size was lower, the distribution was more westerly, and the mean growth was high. In the last three years, the stock strength has become lower, but the geographical distribution is again shifted to the east, and the growth is decreasing.

Growth variation in the Barents Sea capelin stock has been documented earlier, both within and between yearclasses. Differences between yearclasses were discussed e.g. by MONSTAD and GJØSÆTER (1977), and variation in the mean lengths and weights by age-groups sampled in different subareas has been discovered during the joint Soviet/Norwegian autumn surveys to assess the distribution and size of this capelin stock.

GJØSÆTER (1985a) described growth and growth variation as observed between yearclasses, years, geographical subareas and sex in the period 1977 to 1983, and GJØSÆTER and LOENG (1986) discussed the growth variations compared to water temperature at the feeding areas.

Growth variation is essential to management of all fish populations, and particularly so with the capelin stocks. As these stocks consists of very high numbers of small fish, even small individual losses or gains in weight may have a significant effect on the total biomass. In addition, the growth seems to have a strong impact on the population dynamics through length-dependent maturity and high spawning mortality.

This paper aims at a further analysis of the growth variation within and between yearclasses, compared to stock size and geographical distribution.

2. MATERIAL

The investigation is based on data on capelin collected during the annual joint Soviet/Norwegian cruise in the Barents Sea during September. Data from 1974 to 1985 are included. Details on sampling procedures and measurements recorded are given in GJØSÆTER (1985b). Only the age groups two-year-olds and older are used for backcalculation of lengths. To describe the geographical distribution, the Barents Sea is divided into eight subareas, (Fig. 1), but only four or five of these

are usually inhabited by the capelin in September. The samples are weighed by the acoustic abundance estimates for the subareas according to the method outlined by GJØSÆTER (1985b). The essential of this method is to construct a weight for each sample to ensure that distributions constructed on the basis of several samples are representative for the population covered by those samples. The number of fishes in the weighed distributions is an estimate of the number of fishes in the stock. The weighing method rests on the method of bioacoustical abundance estimation of capelin (DOMMASNES and RØTTINGEN 1985, NAKKEN and DOMMASNES 1975, a.o.).
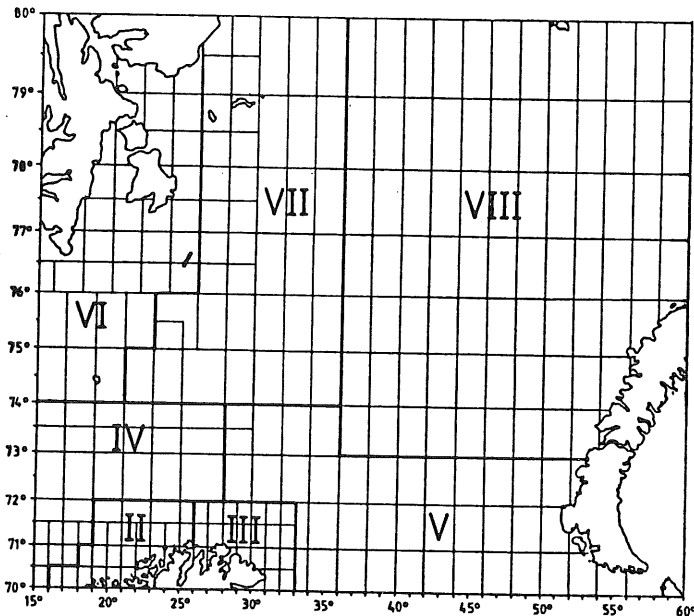

Figure 1. Map covering the Barents Sea showing the subareas (Roman numerals) referred to in the text.

3. METHODS

The method of backcalculation of fish lengths from otolith radia used in this growth study, is described in detail by GJØSÆTER (1985a), and will only be briefly explained here. The basic assumptions underlying the method as used here are:

1. A straight line is a good approximation to the relation between the fish length (L) and a particular total otolith radius (R) when measured at sampling for a group of fishes.

2. A linear relationship between fish growth and otolith growth also applies for each individual fish during its life history.

3. The intercept (a) with the fish length axis estimated from the plot of L versus R for a group of fishes estimates the corresponding intercept for each individual fish in the group.

The relationship between fish length and otolith radius was studied for yearclasses, age groups, areas and sexes separately, using only data from the autumn. All groups were pooled, as no systematic difference could be traced between them. Comparison of the distributions by mathematical methods was impossible because different intervals on the variables was covered in the various groups.

From inspection of the otoliths from unhatched and newly hatched larvae, it appears that the fish length vs. otolith radius relationship does not enter a linear phase before the fish length is about 2-3 cm. For this reason the intercept (a) does not represent the true size of the fish when the otolith radius is zero. However, the sought relationship seems to be linear at the time the first winter ring is deposited in the otoliths, and consequently the backcalculation is not affected by this deviation from linearity. The intercept (a) must, for this reason, be estimated by extrapolation from the data of the linear phase of the relationship. Despite the many models proposed for describing linear relationships between variables whose values have been determined by probability distributions, there is little concensus as to which model should be used in each particular case. The most straightforward method, and perhaps the only one applicable when extrapolation outside the limits of the studied distribution is necessary, is to draw a "line of best fit" by hand.

The pooled distribution, consisting of about 41 000 pairs of measurements, yielded a correlation coefficient of 0.94. This shows that the assumption no. 1 above is fullfilled. An eye-fitted straight line intercected the L-axis at 1.7 cm (Fig. 2).
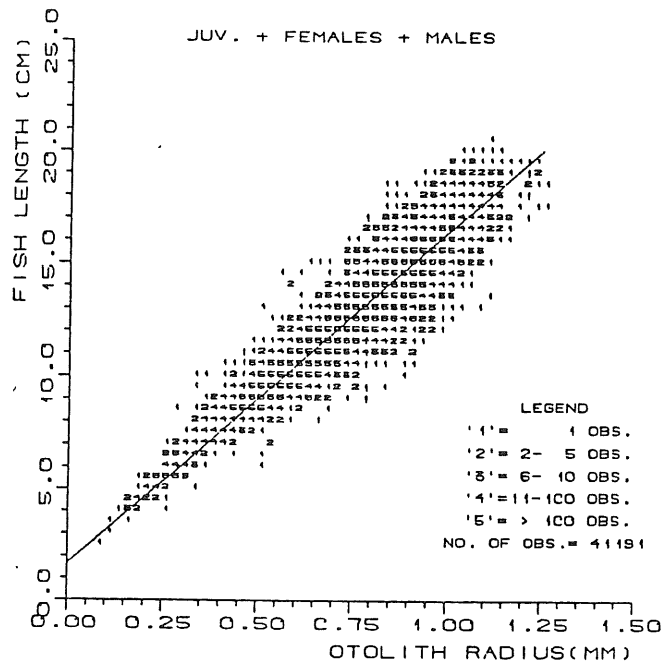

Figure 2. L/R-distribution for the pooled data. A straight line running through the distribution mean with an L-intercept of 1.7 cm is drawn on the figure.

According to this backcalculation method, the relationship between the fish length and the otolith radius for each individual will develop along a straight line between this common intercept to the fish length and otolith radius actually recorded at sampling, and the fish lengths for otolith radia in the winter rings are backcalculated along these individual lines. The following equation was used for the backcalculation:

$$L_n = a + \frac{L_c - a}{R_c} \cdot R_n \qquad (1)$$

where L_n is estimated length corresponding to measured otolith radius R_n of winterring no. n, L_c and R_c are the fish length and otolith radius measured at capture, and a is the intercept of the L-axis for R=0, estimated by the straight line drawn through the distribution. The method is graphically illustrated in Fig. 3.
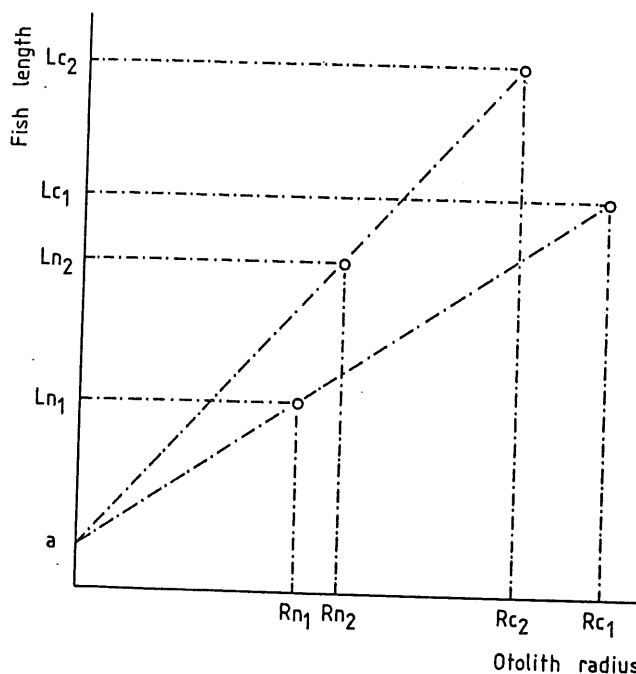

Figure 3. Graphical representation of the backcalculation method. The relationship between the measured and estimated quantities according to equation (1) is shown for two individuals, indexed 1 and 2.

To describe the individual growth of capelin in the current growth season for the various subareas, the backcalculated fish length based on the radius of the outermost otolith winter ring was substracted from the fish length at sampling.

The distribution of these values for all fishes sampled in each subarea is an estimate of the individual growth in length during the current season in that particular area given that the following assumptions are fullfilled:

1. The fishes sampled in a subarea at the cruise in September has inhabited that area during its last growth season.

2. The growth season is ended by the time of sampling.

3. The method of backcalculation gives a correct picture of fish growth in length.

The first assumption could be violated if there was any significant migration during the feeding season. Investigations carried out in the period 1979 to 1982 (GJØSÆTER et al. 1983) showed that the migration towards the feeding areas took place primarily in July and August, and the growth seemed to be low during this period. Also OZHIGIN and LUKA (1985) showed that the main feeding migration takes place during the period from July to Septmeber. It is likely that some growth takes place during the migration to the feeding areas in the northern Barents Sea. Also, some migration will obviously take place inside the main feeding areas, allthough the movement of the capelin is at a minimum during this season. However, it may be argued that the measured densities should be representative for the areas where the most intensive feeding and growth has taken place.

The second assumption, that the growing season is ended by the time of sampling in September, is not completely valid. By comparing the width of the zone from the outer winter ring to the otolith margin in September with the width of the past year's growth zone the next year, it turns out that at average 91% of the otolith growth has taken place by the time of sampling in September. If this affects the fish in all of the subareas equally, it will only affect the absolute values of the growth and have no effect on the shape of the temperature/growth distribution within the year. However, it is impossible to test whether this is the case, because the material cannot be distributed on subareas when analysed the next year. In any case, this effect is probably quite small.

The third assumption is discussed thoroughly in GJØSÆTER (1985a). It could be violated either if the assumption of linearity between fish length growth and otolith growth is invalid, or if the value of the intercept (a in equation 1) is badly estimated. However, the effect of an incorrect intercept will be negligible when comparing only the growth assosiated with the outer part of the otolith, and even small deviations from linearity will have insignificant effect on the estimation of the growth in the last growth season. Any serious violation of the third assumption is thus not likely to occur.

Earlier work on backcalculating lengths of capelin has been conducted on data from the Newfoundland area (TEMPELMANN 1968) and the Barents Sea (MONSTAD and GJØSÆTER 1977, PROKHOROV 1968).

TEMPELMANN (1968) found an R/L-relationship in the form of two straight lines. He did not separate sexes or areas when establishing the relationship. PROKHOROV (1968) also found that two straight lines was the best estimate of the L/R-relationship for the Barents Sea capelin.

MONSTAD and GJØSÆTER (1977) pooled data from various subareas in the Barents Sea, from different seasons and yearclasses. They separated the sexes but found no differences in the R/L-relationships. The two straight lines derived from regressions corresponded to two segment on the R-distribution, namely R less and greater than 0.74 mm respectively. This value was chosen because the R/L-distribution became steeper while the variance became greater above this point. Their R/L-distribution is almost identical to the one derived in the present paper for the younger fish, but a bit steeper for the oldest. For backcalculation they used average radius-measurements and calculated only mean lengths.

4. Results

Stock size estimates divided on subareas are shown in Table 1. Apart from the stock size estimate in 1974, these estimates are based on the weighing procedure described in GJØSÆTER (1985b), and are not identical to the "official" stock size estimates based on age-length keys, which cover the whole area (DOMMASNES and RØTTINGEN 1985). However, the differences are small when the total stock size calculated for the whole area are compared using the two methods. The total stock size in number is seen to vary substantially during the investigated period (Table 1). In 1974, the stock size was very large, containing above 1000 billion individuals, gradually decreasing to between 500 and 800 billion in the period 1976 to 1983. In 1984 it was allmost halved, consisting of about 400 billion individuals, only to be reduced four-fold to about 100 billion individuals in 1985.

Table 1. Stock size estimates per subarea, as no. of 1-year-olds and older (10^7) (numerator), and percentage of total stock (denominator).

YEAR	III	IV	SUBAREAS V	VI	VII	VIII	TOTAL AREA
1974			4499/4	669/1	21612/20	80472/75	107203
1975					19309/21	74097/79	92994
1976			1155/2	97/0	16028/22	54025/76	71305
1977	860/1		17488/25	412/1	12559/18	38072/55	71348
1978		57/0	8438/17	1321/3	17938/35	23017/45	50767
1979			10018/18		14208/26	30413/56	51162
1980			8797/13	554/1	38632/59	17734/27	65606
1981			23503/38	916/1	23658/38	13992/23	58156
1982	2290/3	755/1	38814/49	4289/5	20100/25	13312/17	79511
1983	166/0	500/1	18119/24	3389/4	21497/28	32635/43	74040
1984		118/0	132/0	3921/10	15218/38	21160/52	41493
1985			25/0	774/7	5006/46	5139/47	11110

The geographical distribution has also changed during this period. The percentage of the capelin found in subarea 8 (the northeastern sub-area) during the feeding period (Table 1), is an indicator of an eastern or western distribution. In the years 1974 to 1976, above 75% of the fish was found in subarea 8. From 1977 to 1979, above 45% of the stock was still found in this area. From 1980 to 1982 this quanti-ty decreased from 27% to 17%, indicating a more southern and western distribution during these years. From 1983 and onwards, allmost halv of the stock has again been found in subarea 8.

As the distribution of fish within each subarea may change from year
to year, the stock size within each subarea does not necessarily
reflect the density of fish in the area. To be able to compare growth
and fish density more directly, the mean density of fish expressed in
tonnes per nmi^2 for all the squares containing fish in each subarea
was calculated (Table 2).

Table 2. Estimated fish density per subarea. (Aritmethic mean of the
fish density (tonnes per nmi^2) in the squares containing capelin in
each subarea, based on the calculation of stock size).

| YEAR | SUBAREA | | | | | | TOTAL AREA |
	III	IV	V	VI	VII	VIII	
1974			7.8	13.1	29.0	39.8	33.4
1975					64.0	62.0	62.5
1976			14.2	5.1	36.6	40.2	37.6
1977	6.6		4.6	12.2	45.9	40.3	27.7
1978		1.4	8.5	22.4	39.4	39.4	31.8
1979			2.6		34.4	40.7	27.6
1980			13.7	20.5	119.9	44.3	66.7
1981			16.1	23.5	84.9	22.0	43.4
1982	29.1	49.0	23.1	50.1	49.1	37.7	36.4
1983	2.9	16.7	13.5	19.1	47.1	32.2	28.7
1984		23.0	0.7	16.6	26.3	16.6	19.7
1985			0.3	3.5	9.3	6.1	6.0

The estimated growth in length for the two-year-olds (Table 3) and the
three-year-olds (Table 4) also show a considerable variation from
subarea to subarea and from year to year. The mean growth in each
subarea show a decreasing trend with increasing no. on the subarea,
that is from south-west to north-east.

Table 3 Estimated length growth in the last growing season (cm) for
the two-year-olds. Sexes pooled.

| YEAR | SUBAREA | | | | | | TOTAL AREA |
	III	IV	V	VI	VII	VIII	
1974			2.60	2.83	2.37	2.50	2.47
1975					2.87	2.70	2.73
1976			(2.79)	2.51	2.68	2.67	2.67
1977	(3.68)		2.55	2.43	2.41	2.20	2.27
1978		3.35	3.56	3.27	3.01	2.93	3.03
1979			4.15		3.47	3.31	3.38
1980			3.64	3.08	4.15	3.49	3.92
1981			3.14	5.04	2.96	2.84	2.99
1982	4.75	4.20	3.96	4.25	3.69	3.33	3.71
1983	4.64	4.14	4.39	4.42	3.78	3.37	3.72
1984		4.24	(3.65)	3.06	2.43	2.31	2.43
1985			3.68	3.94	2.76	2.70	2.74

Numbers put in brackets are based on measurements of less than 10
spesimens and cannot be considered representative for a subarea.

Table 4 Estimated length growth in the last growing season (cm) for the three-year-olds. Sexes pooled.

YEAR	III	IV	V	VI	VII	VIII	TOTAL AREA
				SUBAREA			
1974			1.88	2.44	2.10	2.22	2.18
1975					1.88	1.88	1.88
1976			1.94	1.72	1.82	1.89	1.88
1977			(1.95)	2.19	1.98	1.71	1.78
1978		(2.55)		2.37	2.36	2.23	2.28
1979			2.34		2.41	2.18	2.25
1980			2.65	2.43	2.97	2.63	2.79
1981			2.24	3.95	2.36	2.42	2.42
1982	(2.26)	(2.64)	2.17	3.17	2.60	2.06	2.38
1983	(4.02)	(3.07)	3.05	3.66	2.74	2.28	2.68
1984		3.01		2.60	2.39	1.99	2.20
1985			(2.40)	2.98	2.41	2.13	2.20

Numbers put in brackets are based on measurements of less than 10 spesimens and cannot be considered representative for a subarea.

The mean growth of the two-year-olds and the three-year-olds in the total distribution area is plotted versus stock size in Fig. 4. No clear relationship between the two variables is evidenced. The growth is slow in the years 1974 to 1977, at high and intermediate stock sizes, it is fast in the period 1978 to 1983, at intermediate stock sizes, and average to slow after 1983, for small stock sizes.
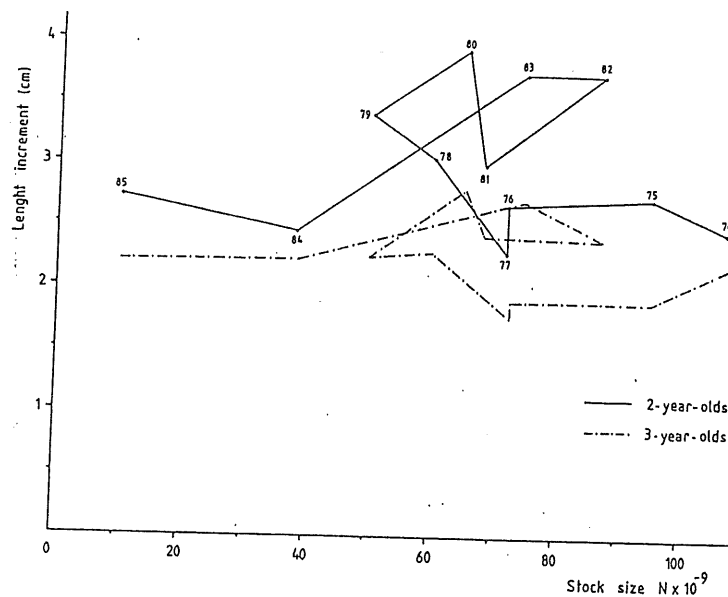

Figure 4. The mean growth of the two-, and three-year-old capelin each year from 1974 to 1985 plotted versus total stock size estimated by acoustical methods. Observation year is shown on the figure.

In Fig. 5 the growth of the two-year-olds (A) and the three-year-olds (B) are plottet versus fish density for each of the subareas in the period. In addition, the same variables are plotted for mean values within years (C). No relationship between growth and fish density can

be traced from these plots. A linear correlation analysis was undertaken for the four groups of data, and the results are given in Table 5.
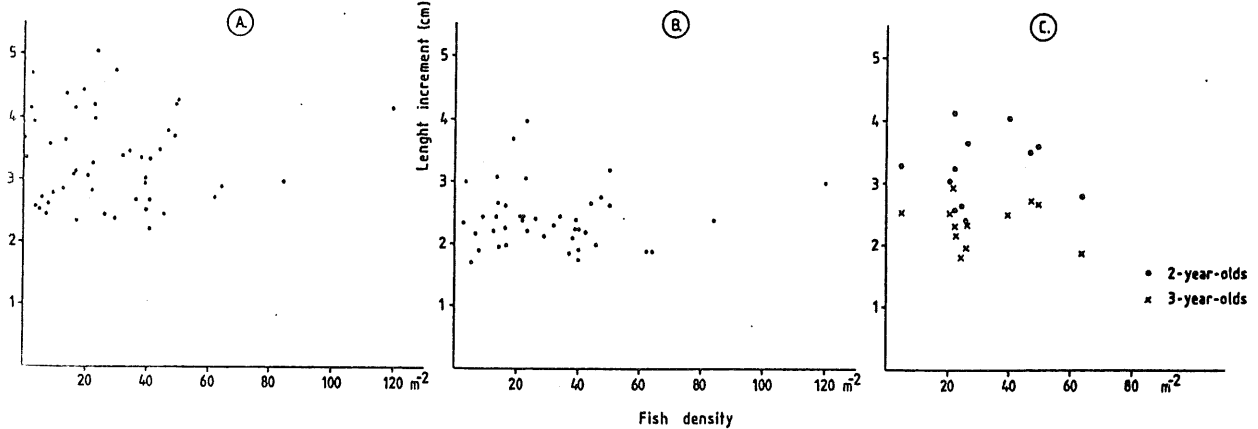

Figure 5. The growth of the two-year-olds (A), and the three-year-olds (B) plotted versus fish density for each of the subareas in the ten year period. Fig. 5 (C) shows a plot of the average values vithin years for the variables.

Table 5. Linear correlation analysis on the relationship between fish density and growth for the four groups of data mentioned above.

Group	r	N
Two-year-olds, all subareas and years	-0.003	49
Three-year-olds, all subareas and years	0.010	42
Two-year-olds, average values for all subareas each year	0.070	12
Three-year-olds, average values for all subareas each year	-0.150	12

These results show that there is practically no correlation between growth and fish density neither as observed for all subareas and years nor for average values within years.

Time series of growth and fish density are shown in Fig. 6. These series confirm the results shown in Fig. 5. Periods of fast growth can be seen to have taken place both in periods of high and periods of low stock density. It should be noted that, under the highest density observed, in subarea 7 in 1980, the growth estiamtes are also among the highest, both for two- and three-year-olds.

In Fig. 7 the growth of the two-year-olds (A), and the three-year-olds (B), are plotted versus subarea number for all years in the observed period. The growth is decreasing with increasing subarea no., that is from south-west to north-east, allthough there is a considerable year-to-year variation.
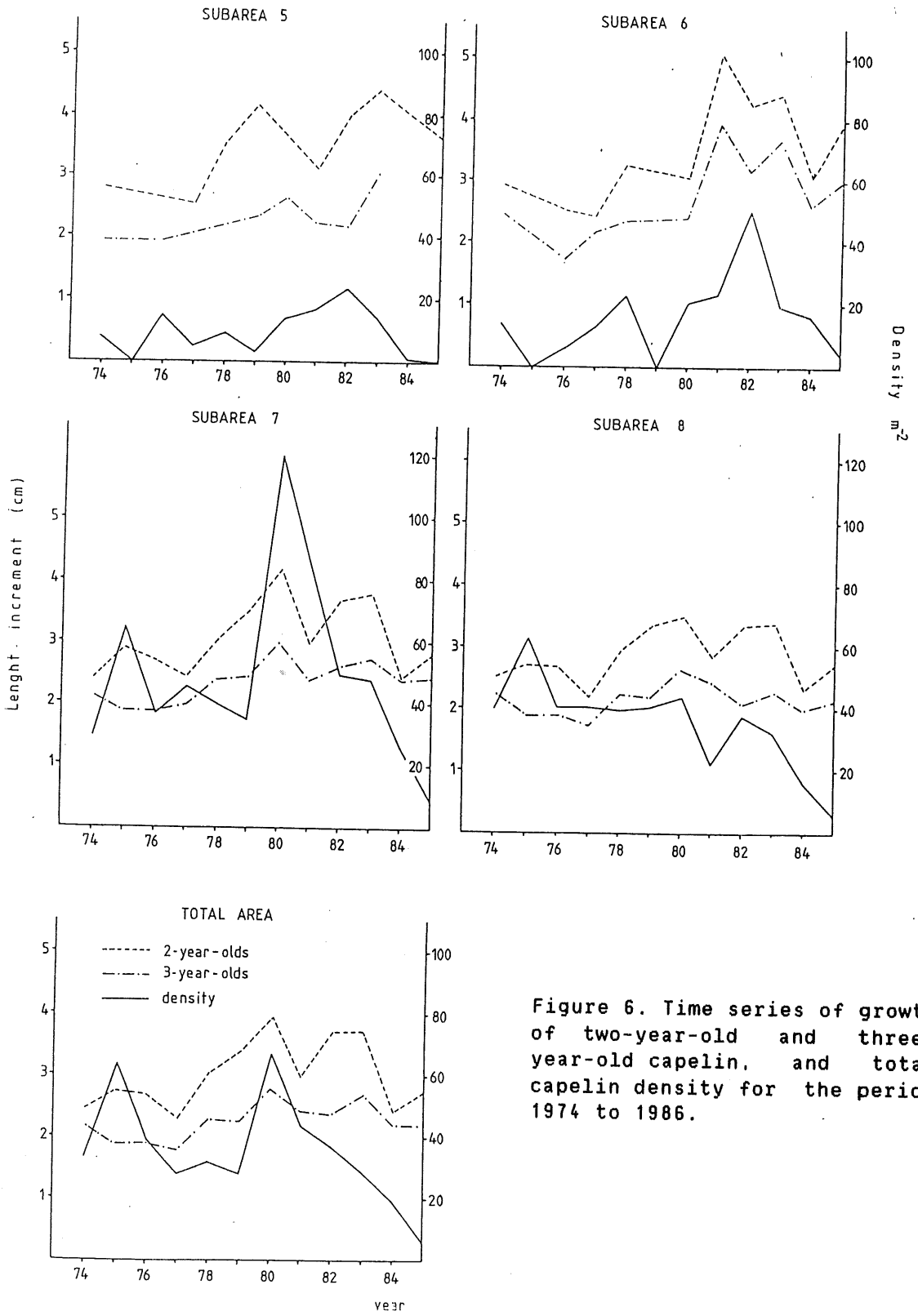
Figure 6. Time series of growth of two-year-old and three-year-old capelin, and total capelin density for the period 1974 to 1986.
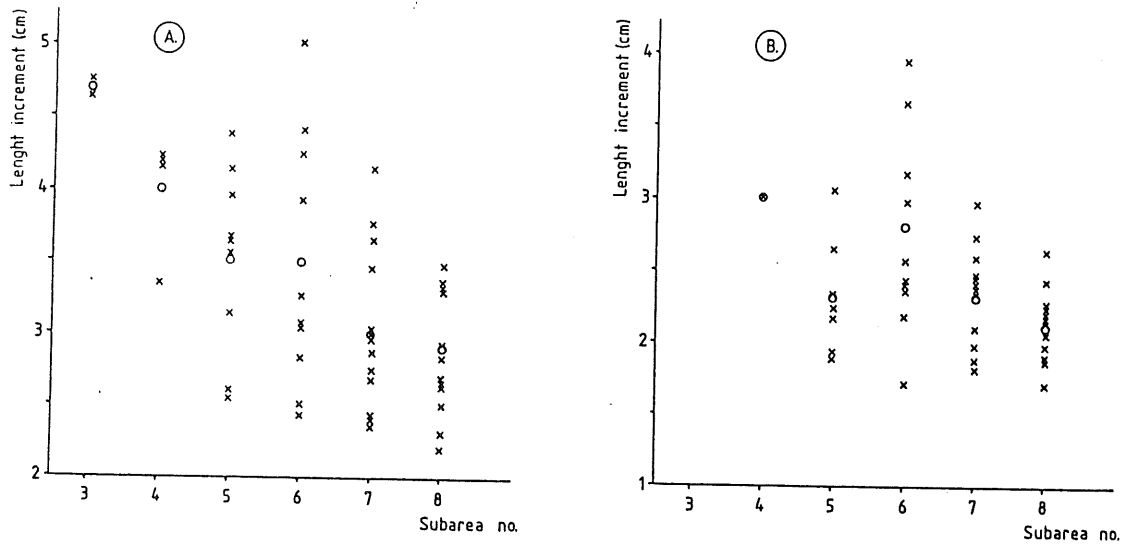
Figure 7. The growth of the two-year-olds (A), and the three-year-olds (B), plotted versus subarea number for all years in the observed period. (X) denotes each observation, (0) mean value for the subarea.

5. Discussion

The present investigation shows no sign of a change in growth, neither as a function of total stock size, nor fish density, at the feeding areas in September.

A density dependent effect, allthough present in nature, could have been overlooked in the investigation. The various sources of error in the methods used, are discussed in the chapter on methods.

Additionally, the growth in length is not the only relevant factor when studying density dependent effects on growth. When the maturity process starts, the gonads will grow at the expence of the growth of the body. The capelin will also store fat to be able to survive the winter and migrate to the coast to spawn. These factors have so far not been taken into consideration.

Density dependent growth will occur only if the stock is resource limited. This situation could be caused by an increase in stock size, and/or a reduction of distribution area of the capelin. However, the same situation would occur if the food resources were reduced beyond a critical level. If a density dependent growth response is caused by a reduced availability of food organsims, either caused by exploitation by the capelin and its competitors, or by abiotic factors, it will not be possible to trace with a method where only the fish density is taken into consideration. Consequently, this kind of density dependence cannot be ruled out by this investigation.

It can be argued that the various sources of errors cannot be responsible for the total lack of correlation between growth and fish density. The following alternatives are then possible:

1. The Barents Sea capelin stock has in the period 1974 to 1985 not reached the population level where food resources became the limiting factor for growth, and consequently, density dependent growth has not occured.

2. Scarcity of food in the feeding season brings about migrations, allowing the stock to exploit the food resources in a larger area than is inhabited by the capelin at the time of the acoustic survey in September, thus obscuring a density dependent factor present in nature.

3. The growth may have been limited by the food supplay, but the limit was not set by the size of the capelin stock.

The biomass of the capelin stock has varied by a factor of ten in the period from 1974 to 1985 (Fig. 4). In this period, the observed mean density of capelin in the subareas lies in the range 0 to 120 tonnes/nmi^2, and in the total area between 6 and 67 tonnes/nmi^2 (Table 2). Investigations carried out in summer from 1979 to 1984 (GJØSÆTER et al. 1983, unpublished cruise reports), indicates that when the capelin moves northwards during summer, the biomass of zooplankton is inversely related to density of capelin. This has led to the working hypothesis that the zooplankton is grazed down by the capelin as the main concentrations moves northwards at typical speeds of three to five nmi/day. The highest density of capelin observed in this migration period was 1400 tonnes/nmi^2 in 1981. Allthough this density is more than ten times the highest concentrations observed at the feeding areas, the fish will only exploit the food resources for a short time while moving through the area, contrasted by the continous exploitations of the food resources at the feeding areas. It is therefore rather unexpected that the highest densities of fish observed in the autumn should lay below a limit where food scarcity should induce a decrease in growth.

The first theory mentioned above seems therefore unrealistic. A more plausible model is the second one, where the feeding capelin exploit a much larger area than is actually occupied by the stock at any single moment. This strategy of resource utilization is difficult to detect when the stock is investigated only ones during the feeding season. This strategy may acount for the absence of any relationship between fish density and growth in our material.

The third theory may also explain why no such relationship is evident. As shown in Fig. 7, there is a clear-cut relation between growth in the present growth season and geographical position at sampling. This indicates that there exists growth conditions, peculiar to each sub-area, which are more or less stable from year to year. That is, the absolute value of the length increment for the fish in a given subarea may change from year to year, but the pattern with decreasing growth from south-west to north-east is seen every year in the period. This indicates that the growth is most likely affected by abiotic factors.

GJØSÆTER and LOENG (1986) found a weak positive correlation between growth and water temperature in the area were the fish was sampled in the autumn. Rather than a simple temperature effect, the temperature may be an indicator of various water masses having peculiar conditions for growth. Both the origin of the water mass, which will determine its content of nutrient salts and primary producers and a parent stock of secondary producers, and the gradual change of the water mass due

to local climatic conditions and mixing with other water masses, wich will determine the conditions for both primary and secondary produ- cers, will influence on the growth conditions for the capelin.

Based on the preliminary observations made during the Norwegian rese- arch project "The growth conditions for the capelin near the ice boar- der" in 1984, HASSEL et al. (1984) established the working hypothesis that the general growth conditions for the capelin in the northeastern Barents Sea is less favourable than in the central and western areas because the mixed water masses in the east has suboptimal conditions for, and contains reduced stocks of, both Atlantic and Arctic zoo- plankton forms.

The third theory may account for this finding of a more or less stable pattern of growth variation from year to year. Most probable, however, a combination of these two mechanisms acts in nature. Abiotic factors sets a limit for zooplankton production in the different areas in the Barents Sea, and may also affect the migration routes and feeding areas for the capelin. In the feeding season, local scarcity of food organisms may force parts of the capelin stock to search for food in nabouring areas.

The conclusions which may be drawn from this investigation is that with the method used, it is not possible to trace any density depen- dent growth in the Barents Sea stock of capelin for the last 12 years. The method has, however, some inadequasies, first of all in determi- ning the representative density of fish pertaining to the period of estimated growth. It seems, though, unlikely that a significant density dependent factor in the growth variation should be completely obscured by the methods used and, consequently, a possible density de- pendent factor has probably played a quite insignificant role in the growth variation observed during the last 12 years.

Rather, the quite significant variation in growth observed during this period, must be ascribed to biotic and abiotic factors working indi- pendent of capelin stock size and density.

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