

GROWTH OF THE BARENTS SEA CAPELIN OF THE YEARCLASSES 1975-1981

By

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ABSTRACT

The method of backcalculating fish lengths based on yearly growth markings in the otoliths is applied to estimate growth of capelin in the yearclasses 1975 to 1981. The Barents Sea is divided into five subareas, and the growth estimates are discussed, in relation to the level of yearclass, year, subarea and sex.

1. INTRODUCTION

Growth differences have been documented for the Barents Sea capelin stock, 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 of age-groups sampled in different subareas has been discovered during the joint Soviet/Norwegian autumn surveys to assess the distribution and abundance of this capelin stock.

Growth variation is essential to management of all fish populations, and particularly so with the capelin stocks. The number of individuals in the Barents Sea capelin stock is very high, and consequently even small individual losses or gains in weight may have a significant effect on the total biomass. In addition, the population dynamic seems to be closely linked to growth through length-dependent maturity and high spawning mortality.

This paper aims at a description of growth and growth variation as observed between yearclasses, years, geographical subareas and sex in the period 1975 to 1983.

2. MATERIALS

The investigation is based on data on capelin collected during the annual joint Soviet/Norwegian cruise to assess the abundance of the Barents Sea capelin stock in September. Data from 1975 to 1983 are included. Details on sampling procedures and measurements recorded are given in Gjøsæter (1984). Only the age-groups two years and older are used for backcalculation of lengths. 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 data are classified according to which subarea the samples were taken from and are weighed by the acoustic abundance estimates for these subareas according to the method outlined by Gjøsæter (1984)

3. METHODS

To describe the mean individual growth of capelin in yearclasses and subareas, fish lengths were backcalculated based on otolith zone radii. By using this indirect method to study growth, some problems with growth studies based on length-at-age observations are partly avoided; as illustrated in the following paragraphs.

The sampling gear selection on small fish will have no effect on the growth estimates, since the size of the youngest age-groups is estimated from otoliths from older fish.

The effects of a possible size selective mortality can be studied by comparing length estimates based on fish from the same yearclass caught at different ages.

The problems induced by differences in when the growing season ends, between years and subareas, are overcome by referring to growth between periods of slow growth represented by the hyaline zones in the otoliths.

Growth of the barents sea capelin of the yearclasses 1975-1981

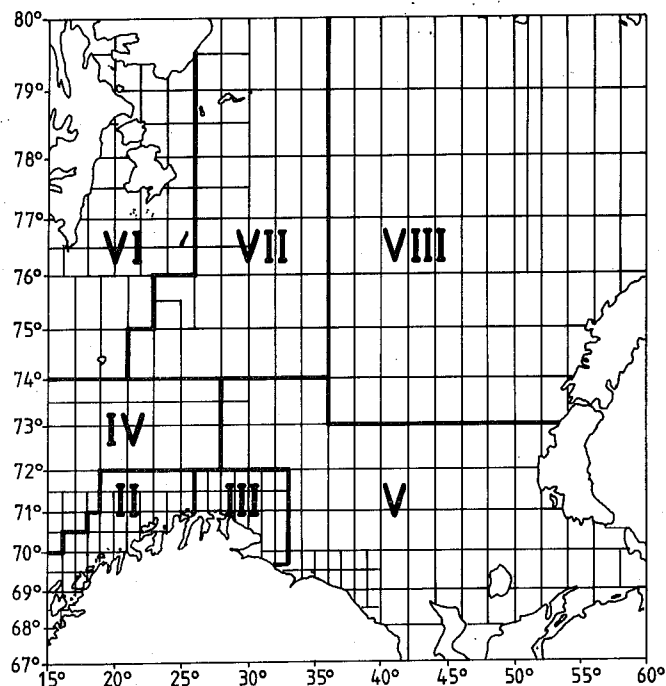


Figure 1. Map covering the Barents Sea showing the subareas (Roman numerals) referred to in the text.

The method of backcalculation of fish lengths from growth markings in scales, otoliths or other hard skeletal parts was introduced by Lea (1910) and has been widely used since then. The method, based on otoliths, can be outlined as follows, when fish length is called L and otolith radius is called R :

If the relationship between fish growth and otolith growth can, to a certain degree of accuracy, be described by a mathematical function, and there exists cyclical growth markings in the otoliths with a known period, then a certain increment in R between these growth markings is associated with a certain increment in L over the time interval delimited by the growth markings.

The relationship between fish growth and otolith growth, is of course, unknown for individual fishes. However, if a strong relationship is found between R and L over certain intervals, this function should be a good approximation of the relationship to individuals over the same intervals.

To avoid possible seasonal variation in the R/L -relationship introducing noise in the sought relation, only fish caught in the same season every year (September/October) were included in the analysis of the relationship. The data were initially divided into yearclass, age-group, sex (males, females and juveniles) and area (east and west of 25° E). Plots of R/L -relationships were made for each of the groups, and for different combinations within each yearclass. The distributions could not be compared using standard mathematical techniques, as each group contained different intervals of R and L , and there was also a clear increase in variance with increasing values of the variates. The two areas were pooled, as no systematic difference could be found by inspection of the plots. Correlation coefficients, (r) , were then calculated for the males, females and juveniles separately, and for the pooled data within each yearclass (Table 1).

The values of r indicate strong linear relationships between R and L for all studied groups. Very little difference can be traced visually between the slopes of the R/L -relationships for the juveniles, males and females. The high linear correlation for the pooled data compared to the separate groups also indicates that the groups may be pooled within yearclass and the R/L -relationship described by a single straight line. It is then reasonable to infer that the same kind of relationship is appropriate for describing the R/L -relation in each individual fish during its growth history. Although inspection of newly hatched larvae reveals that the otoliths do not grow according to this relationship during the earliest growth stages, this linear phase is in effect before the first winterring is deposited, and so will not affect the backcalculation.

The line which best describes the R/L -relationship for individual fishes in the R -interval used for backcalculation, is the straight line through its measured R/L -point at capture and the theoretical fish length at zero otolith radius, which may be considered equal for all individuals within a yearclass. This point must however, be estimated by extrapolation from the data of the linear phase of the relationship. Despite the many models proposed for describing linear relationships between variates whose values have been determined by probability distributions, there is little consensus 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. This method was applied in this study, and lines were drawn running through the mean of the bivariate distributions. The estimated intercepts varies from 14 to 21 mm for the seven yearclasses (Table 1).

An example of the R/L -plots is shown in Fig. 2. The following equation is then used for the backcalculation:

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

where L_n is estimated length corresponding to measured otolith radius R_n of n 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.

TABLE 1. RESULTS OF ANALYSIS OF R/L-RELATIONSHIPS

L and R are the mean length and mean otolith radius, estimated from data collected in September for the yearclasses 1975-1981. r is the correlation coefficient and n the number of pairs of variates.

YEARCL.	GROUP	L	R	r	n	ESTIMATED
		mm	mm			INTERCEPT
1975	juveniles	102.3	.58	.94	2447	
	females	134.0	.79	.79	1229	
	males	136.8	.80	.84	1162	
	SUM	118.7	.68	.94	4838	21
1976	juveniles	97.3	.55	.93	3049	
	females	133.9	.79	.70	800	
	males	136.1	.80	.80	813	
	SUM	110.3	.64	.95	4662	19
1977	juveniles	103.0	.59	.96	970	
	females	144.1	.87	.80	1664	
	males	148.3	.88	.85	1687	
	SUM	136.5	.81	.94	4321	14
1978	juveniles	127.3	.76	.98	583	
	females	135.1	.80	.88	1175	
	males	137.1	.82	.88	1643	
	SUM	134.8	.80	.93	3901	19
1979	juveniles	121.0	.71	.96	1324	
	females	128.0	.76	.89	3148	
	males	129.3	.77	.90	3170	
	SUM	127.3	.76	.92	7642	16
1980	juveniles	82.3	.45	.96	993	
	females	125.3	.74	.89	1919	
	males	126.2	.74	.91	2266	
	SUM	118.0	.69	.96	5178	17
1981	juveniles	81.1	.43	.94	1024	
	females	124.5	.75	.86	1422	
	males	125.3	.75	.89	1832	
	SUM	114.4	.67	.95	4278	21

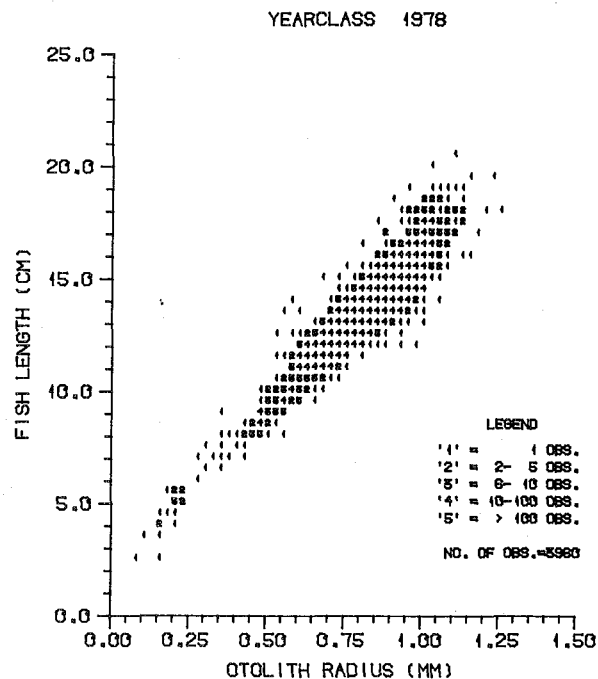


Figure 2. L/R-distribution for the yearclass 1978.

Growth of the barents sea capelin of the yearclasses 1975-1981

Earlier work on backcalculating lengths of capelin has been conducted on data from the Newfoundland area (Tempelmann 1968) and the Barents Sea (Prokhorov 1965, Monstad and Gjøsæter 1977).

Tempelmann (1968) found an R/L-relationship in the form of two straight lines, and backcalculated along these lines. He did not separate sexes or areas when establishing the relationship.

Prokhorov (1965) arrived at similar curves 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 difference in the R/L-relationship. The two straight lines derived from regressions corresponded to two segments on the R-distribution, namely R less and greater than 0.74 mm. 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 ones derived in the present paper for the younger fish, but a bit steeper for the oldest. However, the deviations are rather small, so a rough comparison may be made between the backcalculated lengths and the lengths derived from the present data. For backcalculation they used average radius-measurements and calculated only mean lengths.

4. RESULTS

4.1 Growth of the yearclasses 1975 to 1981, total stock

Backcalculated lengths based on age-groups two to five are shown in Fig. 3 to 8, represented by the distribution mean. Before 1980, sex determination was carried out on individuals more than 12 cm long only. Consequently the length distribution for the two year olds are heavily biased towards greater lengths when separated by sex. For the yearclasses 1975 to 1977 only growth curves based on all fish combined are given (Fig. 3 to 5).

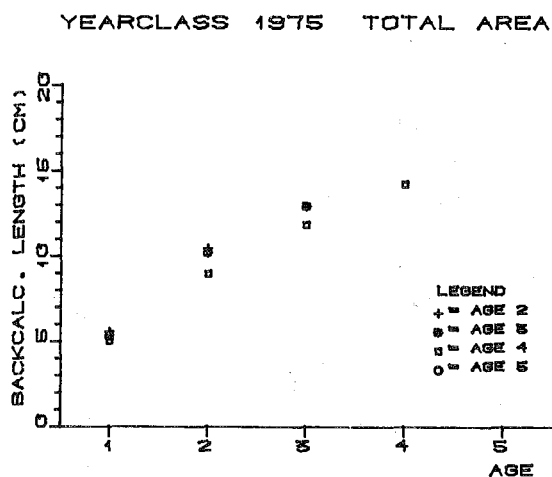


Figure 3. Backcalculated lengths for the 1975 yearclass.

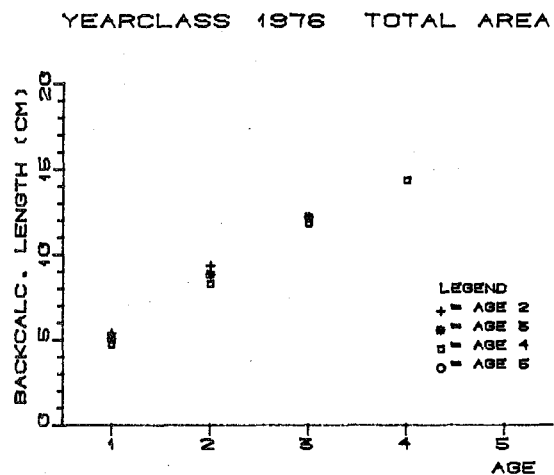


Figure 4. Backcalculated lengths for the 1976 yearclass.

Growth of the barents sea capelin of the yearclasses 1975-1981

Data based on less than 10 individuals are not shown on the plots. The number of fishes in each age-group each year is shown in table 2. Corresponding analyses were not conducted for each subarea separately, as the different parts of the stock do probably not stay in the same area throughout all life stages.

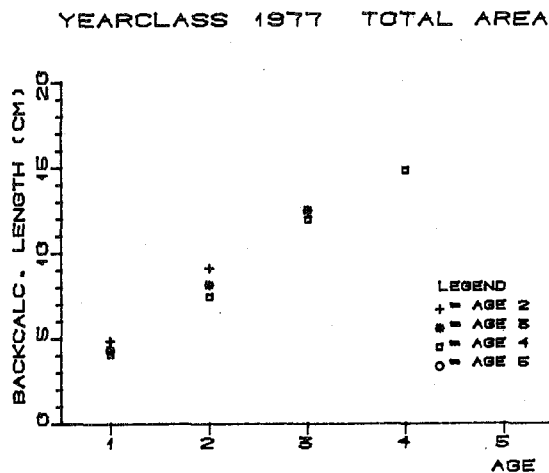


Figure 5. Backcalculated lengths for the 1977 yearclass.

The tables 3, 4 and 5 reveals the magnitude of the growth differences between sexes and yearclasses. The standard deviation given for the backcalculated length distributions is a product of the variation in the underlying R-distributions and the additional variation which may be introduced by the backcalculation.

4.2 Length differences between sexes

At L_1 , there is no great differences between the sexes. When 2-year-olds are measured, the females are an average of 0.4 mm longer than the males. Measured at three- and four years old, the males are an average of 0.7 and 2.8 mm longer than the females (Table 3).

At the time of deposition of the second winterring, the length difference is 0.4 mm in favour of the males when measured at two years old, and the males are 2.3 and 6.5 mm longer as measured in three- and four-year-olds (Table 4).

When the third ring is deposited, the males are longer than the females measured both at three- and four-year-olds, by 4.4 and 7.1 mm respectively (Table 5).

Based on these results, two important observations may be made. Firstly there is a gradual decrease in both L_1 , L_2 and L_3 with increasing age. This is generally known as "Lee's phenomenon", and will be discussed later. Secondly, this phenomenon is seen to be more pronounced for the females than for the males.

Growth of the barents sea capelin of the yearclasses 1975-1981

TABLE 2 NUMBER OF FISHES SAMPLED

YEAR	AGE	SUBAREAS						TOTAL AREA
		III	IV	V	VI	VII	VIII	
1977	2	0	0	25	74	696	1571	2366
	3	0	0	0	30	304	907	1241
	4	0	0	0	12	86	353	451
	5	0	0	0	1	15	62	78
1978	2	0	82	79	281	1012	1092	2546
	3	0	2	0	52	177	287	518
	4	0	0	0	4	15	38	57
	5	0	0	0	1	4	4	9
1979	2	0	0	54	0	511	660	1225
	3	0	0	66	0	221	363	650
	4	0	0	2	0	11	13	26
	5	0	0	0	0	0	0	0
1980	2	0	0	175	144	1051	1111	2481
	3	0	0	156	128	726	1376	2386
	4	0	0	29	12	168	244	453
	5	0	0	1	0	1	4	4
1981	2	0	0	150	159	2531	1829	4669
	3	0	0	43	45	521	528	1137
	4	0	0	5	9	104	157	275
	5	0	0	0	1	0	5	6
1982	2	37	103	886	202	881	1287	3396
	3	1	7	303	56	148	484	999
	4	0	0	14	2	5	17	38
	5	0	0	0	0	0	0	0
1983	2	51	14	297	250	1250	658	2520
	3	4	2	35	69	235	80	425
	4	0	0	2	4	3	0	9
	5	0	0	0	0	0	0	0

TABLE 3. LENGTH AT FIRST WINTER (L_1) (CM).

YEARCLASS	SEX	AGE WHEN MEASURED							
		2		3		4		5	
		\bar{L}_1	SD	\bar{L}_1	SD	\bar{L}_1	SD	\bar{L}_1	SD
1975	F	5.90	.74	5.33	1.01	4.96	.97	(4.18)	.26
	M	5.94	.80	5.37	.96	5.08	.54	(4.37)	-
1976	F	5.92	.66	5.04	.79	4.54	.68	(4.12)	-
	M	5.77	.77	5.11	.82	4.88	.72	(4.60)	.35
1977	F	5.01	.72	4.33	.74	3.90	.71	-	-
	M	5.11	.80	4.32	.74	4.23	.57	-	-
1978	F	4.81	.74	4.70	.76	4.86	.91	-	-
	M	4.71	.76	4.82	.91	5.00	.65	-	-
1979	F	5.24	.89	5.34	.84	(4.14)	.47	-	-
	M	5.15	.92	5.45	.86	(5.01)	.48	-	-
1980	F	5.08	.81	4.94	.87	-	-	-	-
	M	5.03	.82	5.01	.88	-	-	-	-
1981	F	4.95	.83	-	-	-	-	-	-
	M	4.89	.87	-	-	-	-	-	-

Data based on less than 10 individuals are put in parantheses.

Growth of the barents sea capelin of the yearclasses 1975-1981

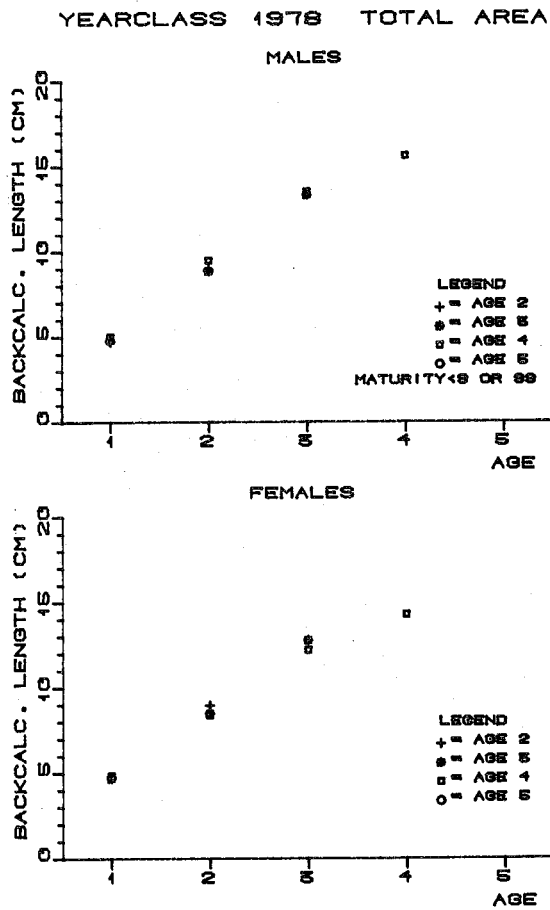


Figure 6. Backcalculated lengths for the 1978 yearclass.

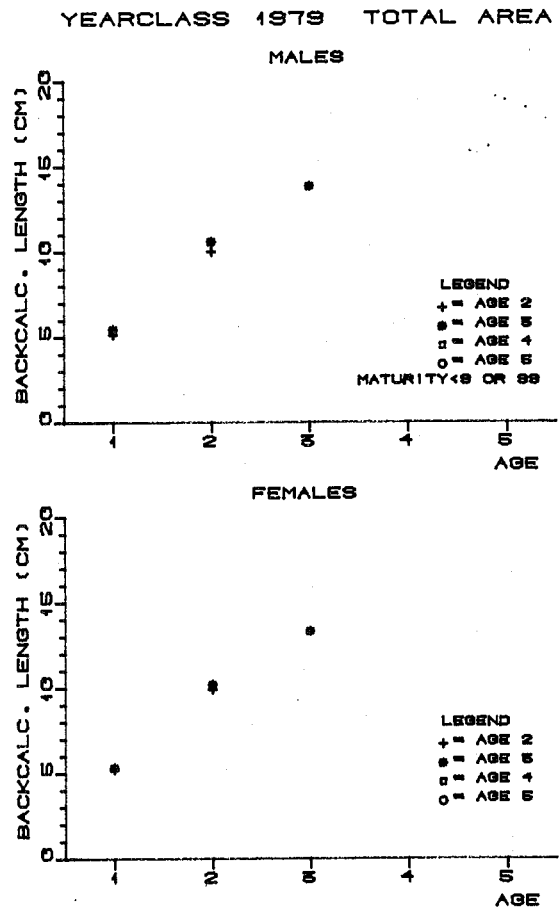


Figure 7. Backcalculated lengths for the 1979 yearclass.

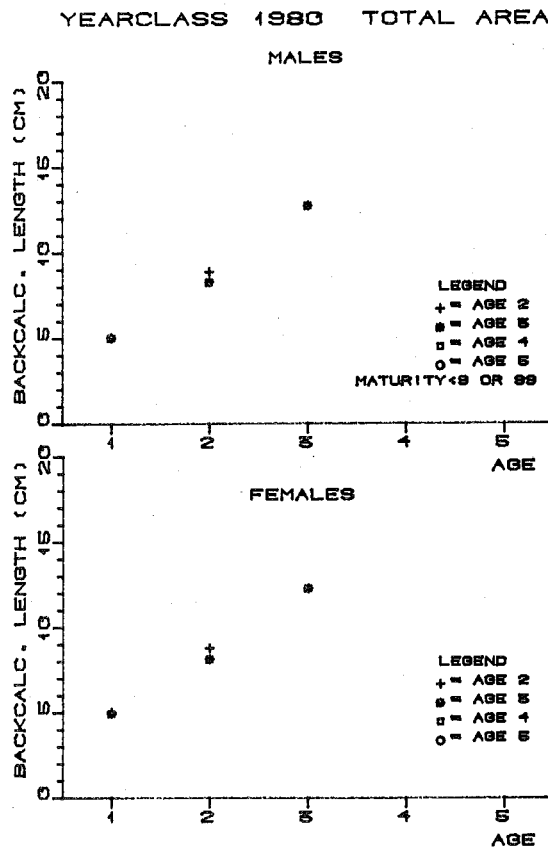


Figure 8. Backcalculated lengths for the 1980 yearclass.

Growth of the barents sea capelin of the yearclasses 1975-1981

TABLE 4. LENGTH AT SECOND WINTER (L_2) (CM).

YEARCLASS	SEX	AGE WHEN MEASURED							
		2		3		4		5	
		\bar{L}_2	SD	\bar{L}_2	SD	\bar{L}_2	SD	\bar{L}_2	SD
1975	F	10.92	.79	10.20	1.55	8.81	1.35	(7.72)	.32
	M	11.06	.94	10.25	1.47	9.09	1.10	(8.27)	-
1976	F	10.16	.83	8.70	1.24	7.98	1.13	(6.03)	-
	M	10.15	1.18	8.95	1.30	8.54	1.14	(7.72)	.52
1977	F	9.44	1.00	8.04	1.48	7.10	1.00	-	-
	M	9.63	1.05	8.24	1.52	7.76	1.30	-	-
1978	F	8.97	1.35	8.49	1.47	8.38	1.25	-	-
	M	8.94	1.47	8.85	1.82	9.47	1.20	-	-
1979	F	9.97	1.25	10.19	1.20	(8.72)	.61	-	-
	M	10.00	1.27	10.58	1.30	(9.74)	.68	-	-
1980	F	8.91	1.54	8.13	1.49	-	-	-	-
	M	8.85	1.67	8.26	1.56	-	-	-	-
1981	F	8.86	1.33	-	-	-	-	-	-
	M	8.89	1.48	-	-	-	-	-	-

Data based on less than 10 individuals are put in parantheses.

TABLE 5. LENGTH AT THIRD WINTER (L_3) (CM).

YEARCLASS	SEX	AGE WHEN MEASURED					
		3		4		5	
		\bar{L}_3	SD	\bar{L}_3	SD	\bar{L}_3	SD
1975	F	12.85	1.12	11.71	.85	(10.29)	.76
	M	13.05	1.37	11.92	.87	(11.85)	-
1976	F	11.97	1.11	11.50	.89	(10.80)	-
	M	12.43	1.18	12.11	1.01	(10.62)	1.45
1977	F	12.27	1.04	11.59	.90	-	-
	M	12.71	1.12	12.30	.96	-	-
1978	F	12.77	1.02	12.19	.82	-	-
	M	13.32	1.36	13.51	.63	-	-
1979	F	13.31	.95	(12.18)	.41	-	-
	M	13.84	1.16	(13.94)	.85	-	-
1980	F	12.28	1.11	-	-	-	-
	M	12.73	1.41	-	-	-	-

Data based on less than 10 individuals are put in parantheses.

Growth of the barents sea capelin of the yearclasses 1975-1981

4.3 Growth in the current year for 2- to 4-year-olds in each subarea

These growth estimates, calculated as the length at sampling minus the backcalculated length from the outermost winterring, are shown for the years 1977 to 1981 in tables 6 to 8, and represented by the distribution mean.

TABLE 6 LENGTH INCREMENTS (CM) AGE-GROUP TWO FOR SUBAREA, YEAR AND SEX GROUP.

YEAR	SEX	SUBAREAS						TOTAL AREA
		III	IV	V	VI	VII	VIII	
1977	F	-	-	2.65	2.20	2.24	2.13	2.19
	M	-	-	(2.62)	2.53	2.43	2.11	2.19
	SUM	-	-	2.65	2.29	2.30	2.12	2.19
1978	F	-	3.32	3.38	3.23	2.92	2.90	2.97
	M	-	(3.66)	4.32	3.16	3.08	2.77	2.97
	SUM	-	3.35	3.48	3.21	2.95	2.87	2.97
1979	F	-	-	4.36	-	3.61	3.53	3.58
	M	-	-	3.71	-	3.52	3.23	3.32
	SUM	-	-	4.30	-	3.58	3.41	3.48
1980	F	-	-	3.60	2.89	3.98	3.47	3.80
	M	-	-	3.76	3.11	4.11	3.54	3.91
	SUM	-	-	3.72	3.02	4.04	3.51	3.86
1981	F	-	-	3.09	4.82	2.91	2.87	2.96
	M	-	-	3.10	5.28	3.07	2.92	3.10
	SUM	-	-	3.10	5.07	2.98	2.90	3.03
1982	F	4.70	3.95	3.98	4.01	3.61	3.29	3.68
	M	4.82	4.12	4.05	4.27	3.79	3.38	3.79
	SUM	4.75	4.03	4.02	4.12	3.70	3.34	3.73
1983	F	4.78	(4.54)	3.89	4.04	3.63	3.22	3.54
	M	4.58	4.04	4.54	4.30	3.62	3.28	3.58
	SUM	4.68	4.14	4.12	4.20	3.63	3.25	3.57

Mean length increments put in parantheses are based on ten or less individuals and cannot be considered representative for the areas.
 - means no data.

Growth of the barents sea capelin of the yearclasses 1975-1981

TABLE 7 LENGTH INCREMENTS (CM) AGE-GROUP THREE FOR SUBAREAS, YEAR AND SEX GROUP.

YEAR	SEX	SUBAREAS						TOTAL AREA
		III	IV	V	VI	VII	VIII	
1978	F	-	(2.46)	-	2.03	2.10	2.03	2.03
	M	-	-	-	2.55	2.54	2.28	2.36
	SUM	-	(2.46)	-	2.28	2.28	2.15	2.20
1979	F	-	-	2.24	-	2.26	2.13	2.17
	M	-	-	2.36	-	2.51	2.16	2.27
	SUM	-	-	2.31	-	2.37	2.14	2.21
1980	F	-	-	2.66	2.40	2.86	2.62	2.72
	M	-	-	2.86	2.59	3.15	2.75	2.96
	SUM	-	-	2.73	2.49	3.00	2.67	2.83
1981	F	-	-	2.11	3.68	2.28	2.35	2.33
	M	-	-	2.25	4.10	2.41	2.43	2.47
	SUM	-	-	2.16	3.90	2.34	2.38	2.39
1982	F	(2.27)	(2.86)	2.10	3.03	2.45	2.00	2.36
	M	-	(2.16)	2.26	3.37	2.81	2.16	2.55
	SUM	(2.27)	(2.66)	2.17	3.21	2.62	2.07	2.39
1983	F	(3.83)	-	2.73	3.23	2.53	2.26	2.46
	M	(4.22)	(3.07)	3.50	3.70	2.97	2.30	2.86
	SUM	(4.02)	(3.07)	3.07	3.55	2.72	2.27	2.63

Mean length increments put in parantheses are based on ten or less individuals and cannot be considered representative for the areas.

' - ' means no data.

Growth of the barents sea capelin of the yearclasses 1975-1981

TABLE 8 LENGTH INCREMENTS (CM) AGE-GROUP FOUR FOR SUBAREAS, YEAR AND SEX GROUP.

YEAR	SEX	SUBAREAS						TOTAL AREA
		III	IV	V	VI	VII	VIII	
1979	F	-	-	(1.62)	-	(2.15)	(1.17)	1.72
	M	-	-	(0.64)	-	(1.65)	(2.33)	2.21
	SUM	-	-	(1.13)	-	1.96	2.09	2.05
1980	F	-	-	1.61	(1.85)	2.19	1.96	2.06
	M	-	-	(2.31)	(1.80)	2.43	2.24	2.36
	SUM	-	-	1.74	1.83	2.29	2.07	2.18
1981	F	-	-	(2.25)	(2.73)	1.69	1.90	1.80
	M	-	-	(1.86)	(3.36)	2.09	1.98	2.10
	SUM	-	-	(1.94)	(3.32)	1.95	1.94	1.97
1982	F	-	-	(1.33)	-	(1.60)	(1.54)	1.52
	M	-	-	(1.45)	(2.72)	(1.71)	(1.44)	1.84
	SUM	-	-	1.40	(2.72)	(1.63)	1.50	1.68
1983	F	-	-	(2.10)	(1.21)	(1.22)	-	(1.23)
	M	-	-	-	(2.11)	-	-	(2.11)
	SUM	-	-	(2.10)	(1.89)	(1.22)	-	(1.24)

Mean length increments put in parantheses are based on ten or less individuals and cannot be considered representative for the areas.

' - ' means no data.

The length increment in the current year is seen to vary between 2.1 and 5.1 cm for the two year olds, but between 2.1 and 3.9 cm for three- year-olds (Table 6 and 7). Despite the considerable overlap in growth between the two age-groups, the two year olds always have a faster growth within area and year. For the four-year-olds, the mean length increments vary between 1.5 and 2.4 cm (Table 8).

The growth difference between the sexes seems to increase with increasing age (Tables 6 to 8 and Figures 6 to 8). While the difference in growth in the second year amounts to only 0.2 mm, the difference increase to 2.3 mm and 4.6 mm in the third and fourth year of life respectively.

4.4 Comparison of growth between areas and years

To facilitate the comparison of growth in areas and years, growth deviations were calculated for each area, based on the average length increments in the area in 1977 to 1983 (A), and the average length increment for all areas (unweighed) each year (B) for males, females and juveniles combined (Table 9 and 10).

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TABLE 9 GROWTH DEVIATIONS (CM) BETWEEN SUBAREAS FOR AGE-GROUP TWO, SEXES COMBINED.

YEAR	SUBAREAS									TOTAL AREA A	
	A	Y	B	A	VI	B	A	VII	B		A
1977	-0.98	+0.31	-1.36	-0.05	-1.01	-0.04	-0.94	-0.22	-1.07		
1978	-0.15	+0.31	-0.44	+0.04	-0.36	-0.22	-0.19	-0.30	-0.29		
1979	+0.67	+0.53	-	-	+0.27	-0.19	+0.35	-0.36	+0.22		
1980	-0.09	+0.15	-0.63	-0.55	+0.73	+0.47	+0.45	-0.06	+0.60		
1981	-0.53	-0.41	+1.42	+1.56	-0.33	-0.53	-0.16	-0.61	-0.23		
1982	+0.39	+0.02	+0.47	+0.13	+0.39	+0.29	+0.28	-0.65	+0.47		
1983	+0.49	+0.12	+0.55	+0.20	+0.32	-0.37	+0.19	-0.75	+0.31		

A = Deviation from average length increment in the area 1977-83

B = Deviation from average length increment in all areas this year.

TABLE 10 GROWTH DEVIATIONS (CM) BETWEEN SUBAREAS FOR AGE-GROUP THREE, SEXES COMBINED.

YEAR	SUBAREAS									TOTAL AREA A	
	A	Y	B	A	VI	B	A	VII	B		A
1978	-	-	-0.81	+0.04	-0.28	+0.04	-0.13	-0.09	-0.24		
1979	-0.18	+0.04	-	-	-0.19	+0.10	-0.14	-0.13	-0.23		
1980	+0.24	+0.01	-0.60	-0.23	+0.44	+0.28	+0.39	-0.05	+0.39		
1981	-0.33	-0.54	+0.81	+1.20	-0.22	-0.36	+0.10	-0.32	-0.05		
1982	-0.32	-0.35	+0.12	+0.69	+0.16	+0.10	-0.21	-0.45	-0.05		
1983	+0.58	+0.17	+0.46	+0.65	+0.16	-0.18	-0.01	-0.63	+0.19		

A = Deviation from average length increment in the area 1977-83

B = Deviation from average length increment in all areas this year.

With few exceptions, an increase in growth has taken place during the years 1977 to 1983, which is also reflected in the weighed mean length increment values for the total stock (Table 6 to 8). The length increment deviations thus show an increasing trend with time, but the growth reach maximum in 1980 and level off afterwards (Table 9 to 10).

4.5 Growth index of areas and years

Based on the data given in Tables 6 and 7 a "growth index" was calculated for each area each year (Table 11). The index is the unweighed mean length increment of the age-groups two and three, both sexes combined, for each area and year.

The growth indices are meant as a basis for comparison between subareas and years. It is calculated from the length increment in the current year for age-group two and three only, as the four-year-olds are not always represented in all subareas. Backcalculated length increments for the 0- and 1-group are also not included, as there may

be some doubt that the capelin remains in the same area from age 0 to age 3.

TABLE 11. GROWTH INDICES (UNWEIGHED MEAN LENGTH INCREMENTS FOR BOTH SEXES COMBINED IN AGE-GROUP TWO AND THREE) FOR SUBAREAS AND YEARS.

YEAR	SUBAREAS				MEAN	TOTAL AREA
	V	VI	VII	VIII		
1978	-	2.75	2.62	2.51	2.63	2.59
1979	3.31	-	2.98	2.78	3.02	2.85
1980	3.23	2.76	3.52	3.09	3.15	3.35
1981	2.63	4.49	2.66	2.64	3.11	2.71
1982	3.10	3.67	3.16	2.71	3.16	3.06
1983	3.60	3.88	3.18	2.76	3.36	3.10
MEAN	3.17	3.51	3.02	2.75		2.94

5. DISCUSSION

5.1 Growth of the yearclasses

With the exception of the 1978 yearclass, all yearclasses show discrepancies between lengths backcalculated from different age-groups. The differences in L_1 and L_2 backcalculated from two- and three-year-old fish are small, except for the 1977-yearclass, where the three-year-olds show smaller L_1 and L_2 than the 2-group. The four-year-olds, however, have smaller backcalculated lengths than the younger age-groups.

The term "Lee's phenomenon" has been applied to discrepancies of this type, named after Rosa Lee who was the first one to investigate possible causes of the phenomenon. Different explanations have been proposed for this feature of backcalculated growth curves, among which a length selective mortality may be most common.

It is believed that capelin in the Barents Sea experience mass mortality after spawning, although there is not full agreement over whether the mortality is total or not. This mass mortality is very likely length selective, as the maturation of individuals is known to be partly length dependent, at least for the females (Tjelmeland and Forberg 1984). Such a mortality would work in the following way: the larger individuals among the three year olds, which also probably were among the largest at ages one and two, and therefore also have the greatest R_1 and R_2 , will spawn and die, thus removing the upper part of the distribution² of R_1 , R_2 and R_3 for this yearclass, making the mean radii smaller for the surviving part of the yearclass. At age four, the largest among the survivors will mature, spawn and die, thus again removing the upper part of the R-distributions, making the mean R_1 , R_2 and R_3 still smaller. This will continue until there are no survivors left. The mean L_1 , L_2 and L_3 calculated from otoliths from individuals of increasing age, will decrease correspondingly, but will always be representative for the part of the yearclass surviving until sampling.

There is also a possibility for a length-selective fishing mortality. The importance of this is difficult to assess. If the spawning mortality is total, a length-dependent fishing mortality on the spawning stock will have no effect. Conversely, in the autumn fishery, it could affect the calculated growth curves. However, the part of the total stock exploited in this fishery is almost exclusively the part that, in any case, would have entered the spawning stock the next spring, and again, if the spawning mortality is total or nearly so, this will have little or no effect.

In addition to a length selective mortality, sampling error is another possible cause of Lee's phenomenon. If the samples were biased towards greater individuals for the two-year-olds and/or towards smaller individuals for the oldest age-groups, this would have the observed effect on mean R , measured for each age-group. Biased sampling could be caused by gear selectivity and/or behavioural differences of age-groups. Unfortunately, we have little exact knowledge of the gear selectivity for capelin in the utilized trawls. The smallest individuals are thought to be underestimated, and this has led to the decision not to include the 0- and 1-group capelin in analyses where an unbiased length distribution is required. However, it is unknown whether gear selectivity on length also might effect the older age-groups. Behavioural differences related to length, either directly or indirectly through length-dependent maturation could for example imply different vulnerability to the sampling gear by dept stratification or amount of schooling. Unfortunately, too little is known about possible mechanisms, and their effect on the sampling. This possibility must be kept in mind when inquiring into the causes of the Lee's phenomenon.

A third possible mechanism for the observed phenomenon is an inadequate backcalculation technique. To test if this explanation could apply for the present study, the mean backcalculated lengths were compared with the corresponding mean otolith radia for the different yearclasses. The result for the yearclass 1975 is shown as an example (Table 12). The decrease in backcalculated lengths is accompanied by a large decrease in otolith radia. This makes it improbable that the decrease in backcalculated lengths is an artifact caused by methodological errors. For this to happen, the L/R -ratio among the fishes in the first winter had to decrease in proportion to the number of years left until sampling. This is, of course, just a theoretical possibility. A methodological error can, however, change the effect a certain change in radius will have on the backcalculated length. It can be shown that, if, for example, the real L/R -relationship was curved either upwards or downwards for increasing values of R , while the intercept of the L -axis was correct, the method used would lower the magnitude of the Lee's phenomenon. The effect of an incorrectly estimated L -intercept would vary with the sign of the difference between true and estimated values. A too low estimated L -intercept would cause a too high range in backcalculated lengths for a given interval on R , and vice versa. The magnitude of this error will decrease for increasing values of R , so while this could have some effect on backcalculated L_1 , the effect on L_2 and L_3 would probably be negligible.

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TABLE 12 CORRESPONDING VALUES OF R AND BACKCALCULATED L

YEARCLASS	AGE	R ₁ mm	L ₁ mm	R ₂ mm	L ₂ mm	R ₃ mm	L ₃ mm
1975	2	.229	54.0	.562	101.8	-	-
	3	.215	53.3	.538	101.9	.721	129.0
	4	.194	50.4	.454	89.9	.644	118.5
	5	(.151)	(42.0)	(.410)	(77.7)	(.599)	(104.2)

It is reasonable to conclude that a length dependent spawning mortality stands as the most probable main cause for the Lee's phenomenon in this stock. If this hypothesis is right, the age at which Lee's phenomenon appears and its magnitude may give some information on the amount of spawning at different age groups.

The growth differences between sexes seems to start at age three and increase thereafter with age (Tables 3 to 8). Lee's phenomenon is more pronounced among the females (Tables 3 to 5), which, if this is caused by length-dependent mortality, implies that females are more affected by this selection than are the males. Various reasons may explain this difference. The females may have a higher spawning mortality rate than the males. Forberg (1982) has shown that female capelin have the potential to spawn more than once, while it is doubtful whether the males have the same potential. Consequently, the males should have a lower probability of surviving the spawning than the females have. However, the males may start the maturation process later, resulting in a lower maturity rate for the youngest age-groups.

It is difficult to test these different hypotheses by means of independent data. Also, a thorough discussion of possible reasons for the observed differences in Lee's phenomenon lies beyond the scope of this paper. It can readily be seen however, that the amount of Lee's phenomenon is not directly linked to length (Tables 3 to 5).

Monstad and Gjøsaeter (1977), backcalculating lengths for the 1967-70 yearclasses, found L₁'s about 7% higher than those calculated for the yearclasses 1975 to 1981. L₂ was, however, an average of 15% higher than those calculated in the present study. As for the L₃'s, the mean value for the 1967 - 70 yearclasses was about 5% higher than for the 1975 - 80 yearclass. These differences are not an artifact caused by different backcalculation methods, as they are confirmed by comparison of corresponding mean otolith radia. This indicates a higher mean growth rate of the yearclasses in the period 1967 to 1973 than of those in the period 1975 to 1983. However, Monstad and Gjøsaeter (1977) did not take into account possible spatial growth variation, nor did they weigh the data by abundance. A direct comparison of the results should therefore be avoided.

The growth pattern of the yearclasses 1975 to 1981 show some differences (Fig. 3 to 8). This can probably be partly explained by changes in the growth conditions from year to year affecting the yearclasses at different ages. For instance in 1980 the 0-group had an above average growth, the two-group had the best two-group growth in the studied period, and the three-group had the highest growth measured for a three-group, with the effect that the 1978 yearclass, while at age three were among the smallest, got an average length well above the age four average.

5.2 Growth in current year

The growth estimates (Table 6 to 8) cover the period from last winter to sampling in September. There may be some variation in the time of termination of the growing season between areas and years, and this may put some restrictions to the use of these calculated length increments as estimates of the last year of growth. The major part of the growth has, however, probably taken place before this time, so the calculated length increments may give a good indication of the growth in current year. Only in 1977 were more than 10 individuals of five year old fish sampled (Table 2), so nothing can be said about the growth of the five-year-olds. Also the four-year-olds are very poorly represented in the catches, reflecting the low number of older fishes in the stock in the last years.

The highest values are found in the southern part of the sea, areas three, four and five, and the northwestern area, no. six. As the abundance of fish is always highest in the central and northeastern areas, the mean growth for the total stock is only slightly higher than for the two areas seven and eight of slow growth. The length increment values for the total stock of two-year-olds varies between 2.2 and 3.9 cm, the three-year-olds vary between 2.2 and 2.8 cm, and the four-year-olds between 1.7 and 2.2 cm during the years covered, with arithmetic mean values at 3.4, 2.4 and 2.0 cm respectively.

The growth differences between the sexes (Table 6 to 8) is negligible among the two-year-olds, amounting to 0.2 mm in favour of the males. As three year olds, the males show a faster growth in all areas and years, at an average 2.5 mm. The same applies for the four-year-olds, where the difference amounts to 3.5 mm.

Generally the differences between areas are rather small, but 1981 is an exception, as this year the growth in area no. 6 is about 60 % higher than in the other areas for age-groups two to four. In 1980 this area was also exceptional, in that the growth in area 6 is the lowest measured this year.

These results show that although a pattern of growth variations between areas may be recognized, unpredictable variations occur, whose mechanisms are as yet poorly understood.

The comparison of growth between years and areas (Table 7 and 8) shows similar trends for the two- and three-year-old fish. The within-area deviations (A in the tables) are generally negative in the first years of the investigation, but also as late as in 1981 for all areas except no. six. Also, in the last two years, the deviations are generally positive, indicating a general increase in growth of age-groups two and three during the period. The within-year-deviations (B in the tables) reveal that the growth, almost without exception, is lowest in areas seven and eight.

To facilitate the comparison of growth between areas and years, the arithmetic mean of the length increments of two- and three-year-old fish was calculated (Table 11). These "growth indices" (GI) will give an overall picture of the growth variation in space and time. The average GI over the time period for each area and over all areas each year was also calculated (Table 11). Based on these results the areas can be ranked in the order of best growth from six, five, seven and eight. The two areas in the southwestern part of the sea (not included in table 11) is difficult to compare with the others as only with age

group two in the last few years was a significant number of fishes sampled. These years however, the growth seems to have been very good (Tables 6 and 7). A ranking of years would put 1980, 1982 and 1983 on top and 1978, 1979 and 1981 on bottom.

The mechanisms behind these growth differences are unknown. Environmental factors like temperature may be important (Gjøsæter and Loeng 1984), but also factors as competition for food, parts of the population with different growth capacity inhabiting different subareas, maturity and mortality affecting the subpopulations differently etc. could affect the growth in various ways.

6. CONCLUSIONS

Based on the results from this investigation, the following main conclusions may be drawn.

1. The otolith radia and the fish lengths are linearly correlated, and thus the method of backcalculating fish lengths from otolith growth zone radia along straight lines can be applied.
2. The growth is higher in males than in females after the second year of life.
3. The growth decreases with increasing age from the first year of life.
4. The growth is generally higher in the western and southern parts of the Barents Sea than in the northern and eastern parts.
5. The growth is higher in the years 1980 to 1983 than in the period 1977 to 1979.
6. A considerable amount of "Lee's phenomenon" is found. It could be caused by a length dependent spawning mortality, but factors as length selective fishing mortality or sampling errors may also play an important role.
7. Lee's phenomenon is more pronounced among the females than among the males, which can be caused by a higher spawning mortality rate among the females and/or a lower maturity rate among the males.
8. The growth variations are similar in all age-groups during a growth season within a subarea. That is, the growth variations are related to area and/or year, which indicates that environmental factors affect the whole stock in a similar way.

As mentioned introductory, understanding the growth and growth variations in the capelin stock is essential to the management of the resource. If a growth rate could be predicted for the next year based on expected environmental changes, the management could be greatly improved. The growth will affect both the number of fishes entering the spawning stock next year, the number remaining in the immature part of the stock, the spawning stock's gain in weight until the time of spawning, and the growth of the immature part of the population until the autumn fishery next year (Tjelmeland 1984).

The description of the historical growth patterns and growth rates contained in this paper does not allow for such forecasting. However, by comparing these results with relevant data on changes in environmental factors, an understanding of which factors affect the growth could possibly be gained. In the meantime, a longer time series of historical growth should be collected, allowing for an improved base of average historical growth rates for modelling future growth.

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