

THE EFFECT OF AMBIENT TEMPERATURE ON THE SPAWNING MIGRATION OF CAPELIN

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ABSTRACT

The model presently in use for management of the Barents Sea capelin stock may be considerably improved by utilization of biological information from the spawning stock. The distributions of length and age for capelin during its spawning migration exhibit considerable geographical variation. Previously, it was not possible to construct reliable length and age distributions based on direct measurements for the spawning stock. The present paper seeks to develop a method for estimating the geographical distribution of the spawning migration, once the initial distribution and the sea temperature is known. To do this, a theory for spawning migration is developed, and the east-west component of the migration pattern is estimated. Possible relationships between the estimated migration and the sea temperatures at onset of migration and sea temperatures at the end of migration are discussed.

INTRODUCTION

The most important part of the mathematical model presently in use for management of the Barents Sea capelin stock is the submodel for dividing the total population as measured in the autumn, into

- 1) a maturing part that will spawn the next spring, and
- 2) an immature part that will not take part in the spawning migration (TJELMELAND 1985).

This model is constructed by comparing the modeled immatures next autumn to the measured autumn stock (HAMRE and TJELMELAND 1982). By performing a similar procedure comparing the modeled mature stock to the measured spawning stock, an independent check of the model could be made. Also, calculations involving only half a year simulation should be preferred to calculations involving one year simulation.

Although having been tried (HAMRE and TJELMELAND 1982) such a use of data from the spawning stock is difficult because it is not possible to construct reliable distributions. The reason for this is that both the distributions for age and length may be very different in the western and eastern part of the spawning migration. A method for weighting these distributions properly, in order to obtain a distribution for the spawning

stock based on biological samples from the spawning stock, does not exist.

The present paper is an attempt to construct such a method. The maturing part of the stock, as measured in the autumn, is transformed into an eastern and a western spawning stock component using a new theory for the spawning migration. An average migration pattern for the years 1980-1985 is estimated by comparing the mean length differences between modeled and measured stock in the eastern and western spawning area, respectively. One parameter for an annual east-west deviation from the migration pattern is then estimated year for year. This deviation parameter was found to correlate with the hydrographic conditions. This makes it possible to forecast the geographical distribution of the spawning migration for the following spring once the geographical distribution in the autumn and the temperatures are known.

The implications of this method for management are greater than just a safer basis upon which to construct models for the maturing of capelin. Also, a quantification of the east-west parts of the spawning migration is important in order to quantify the overlap between capelin and cod. Furthermore, an important feature is the possible correction of the recruitment relation which can be made. A western spawning gives rise to larvae having different surviving and growth conditions than an eastern spawning.

MATERIALS AND METHODS

OZHIGIN and LUKA (1985) treated the geographical distribution of spawning extensively, and demonstrated that during warm years, capelin tend to have a more easterly spawning than for cold years. However, in the present paper the scope will be widened to also include a quantification. In order to do so, a verbal theory for migration that can serve as a basis for quantification must first be constructed.

The spawning stock will be defined as the stock consisting of fish having a maturing stage at or above a certain level, as measured in the autumn. The new maturity scale based on microscope investigations of eggs will be used (FORBERG and TJELMELAND 1985, FORBERG 1982). Thus, the spawning stock in this paper will be an ambiguous concept, dependent on which stage is used. The use of the new maturity scale leads to the restriction that only females may be used. Also, only 3 year old fish during the autumn will be studied in order to simplify the investigations. This age group, which will be 4 years in the spring, constitute the major part of the spawning stock. Consequently, this age group gives the most comprehensive data base. Thus, for this paper, the geographical distribution of mature 4 year old females was studied, and the dependence on the temperature regime is discussed.

Throughout this paper, the geographical distribution of capelin will be based on the area division shown in Fig. 1. Table 1 shows the mean lengths of maturing 3 year old capelin in September. In constructing the table, the computer program presented at the Soviet-Norwegian symposium in 1984 is used (GJØSÆTER 1985). The area division (Fig. 1) is also the same as used in the previous symposium. The method of field sampling is described by DOMMASNES and RØTTINGEN (1985) and GJØSÆTER (1985).

With only one exception (stage IIIc, 1983), the mean lengths are always greater in area 7 than in area 8 for fish within the same maturity stage. There is thus no one-to-one correspondence between length and maturity, even for fish within the same age group. Environmental factors are most

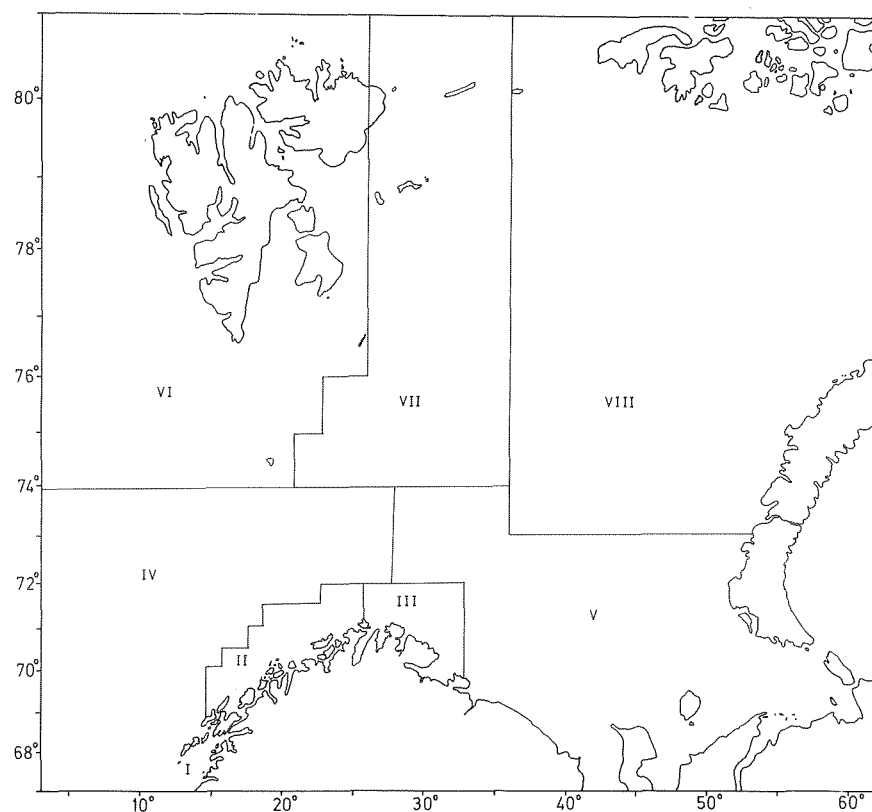


Fig. 1. Map of the Barents Sea showing the geographical division referred to in the text.

probably governing the relative speed between length growth and maturation. With the exception of 1980, the mean lengths are also greater in area 6 than in area 7. Thus there is an increase in length from east to west for all maturity stages.

Table 2 shows the mean length from biological samples of the spawning stock. Only fish of maturing stage 3 or greater (old stage, GJØSÆTER 1985) were used in order to avoid accidental catches of immature fish. Data from research vessels as well as from commercial catches were used. The sampling from commercial catches was described by GJØSÆTER (1985). Fig. 2 shows the geographical distributions of the samples used. With the exception of 1984, March samples from areas 2 and 3 have been used. For 1985, two samples from area 4 were also added to the samples from area 2. For 1984, February samples were used due to insufficient sampling during March.

During 1981, 1983, and 1984, the fish were longer in the western area 2 than in the eastern area 3. The mean length differences were, however, much smaller than would be expected from the differences in mean length between areas in the autumn. In 1982 the fish were longer in the eastern area. These figures are not consistent with the simple theory of migration which assumes that fish being found in the eastern parts of the sea during the autumn will spawn in the eastern parts of spawning area and vice versa.

DISCUSSION

A theory for the spawning migration of capelin

In order to explain these data, the following migration theory is suggested:

Table 1. Number (N, 10⁶ ind.) and mean length (l, cm) of maturing 3 year old female capelin.

1980	Area V		Area VI		Area VII		Area VIII	
	N	l	N	l	N	l	N	l
IIb	4305	15.32	801	15.06	30906	16.19	34873	15.37
IIIa	3588	15.40	567	15.21	28061	16.30	29456	15.49
IIIb	2501	15.58	285	15.39	23887	16.48	16807	15.71
IIIc	1251	15.77	16	15.75	15226	16.75	5825	15.88
1981	Area V		Area VI		Area VII		Area VIII	
	N	l	N	l	N	l	N	l
IIb	477	15.21	499	17.89	14305	15.79	6766	15.60
IIIa	405	15.27	499	17.89	12505	15.96	6037	15.66
IIIb	234	15.60	499	17.89	9153	16.21	3807	15.84
IIIc	36	16.50	325	18.06	5314	16.41	501	16.00
1982	Area V		Area VI		Area VII		Area VIII	
	N	l	N	l	N	l	N	l
IIb	7339	15.60	3029	17.41	11590	16.42	12848	15.71
IIIa	6815	15.62	3029	17.41	11222	16.49	12088	15.73
IIIb	2983	15.82	3029	17.41	10642	16.56	7145	15.88
IIIc	517	15.90	2661	17.61	6311	16.79	1359	16.25
1983	Area V		Area VI		Area VII		Area VIII	
	N	l	N	l	N	l	N	l
IIb	635	16.02	373	16.08	8431	15.69	3194	15.04
IIIa	578	16.03	373	16.08	7576	15.81	3012	15.07
IIIb	55	16.59	175	16.82	6318	15.92	1838	15.15
IIIc	0		136	16.86	2344	16.06	518	16.16
1984	Area V		Area VI		Area VII		Area VIII	
	N	l	N	l	N	l	N	l
IIb	0		2108	16.09	3964	15.95	7090	15.29
IIIa	0		1967	16.29	3743	16.07	6242	15.29
IIIb	0		1568	16.49	2875	16.40	3493	15.61
IIIc	0		715	16.91	1785	16.73	1285	15.57

Table 2. Mean length (l, cm) and number of specimen (N, 10⁶ ind.) of mature 4 year old female capelin. Data from March samples.

Year	Area 2		Area 3	
	l	N	l	N
1981	16.34	424	16.29	658
1982	16.49	305	16.72	612
1983	16.62	299	15.93	220
1984	16.28	425	15.74	191
1985	15.92	152	16.20	187

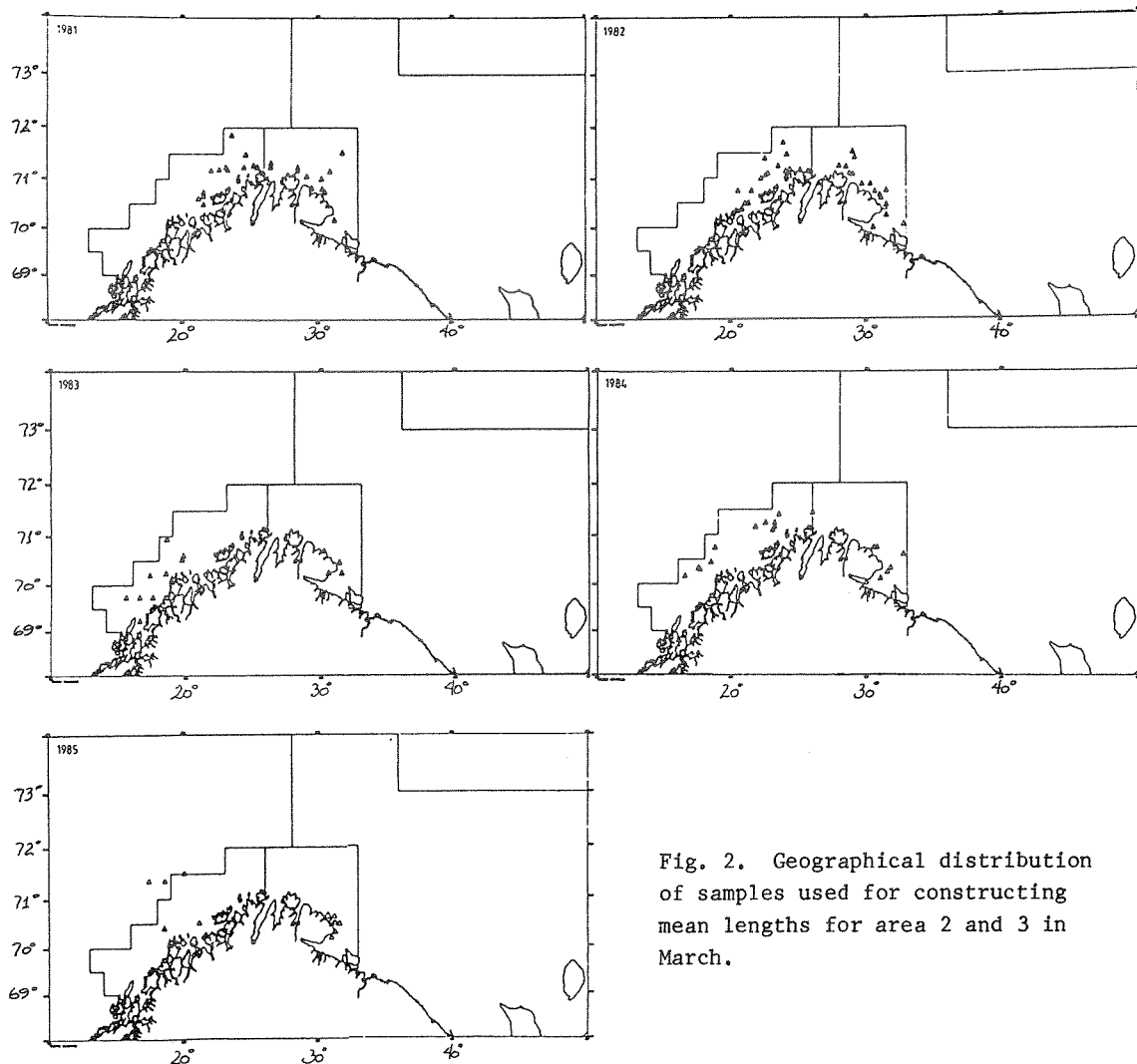


Fig. 2. Geographical distribution of samples used for constructing mean lengths for area 2 and 3 in March.

Fish at the most mature stages during the autumn will start their spawning migration earlier than fish at lower maturity stages.

And in conjunction with this:

The spawning migration is temperature dependent. Higher temperatures in the sea leads to migration routes which are further west.

We know from hydrographical observations (LOENG 1984) that the Barents Sea is cooled down during the winter period, and reaches the coldest temperature about April. The decrease in temperature during this period is about one degree, comparable to the temperature difference between areas. Loeng's results are, in this respect, considered generally valid. This means that during the whole period of spawning migration, the isotherms move westwards. Fish having a late start for spawning remain in colder water masses, and will eventually seek more western migration routes.

The theory above together with the fact that the sea is being cooled during the migration period implies that the fish will be of greater length in the eastern part of the spawning stock.

The length differences observed in the spawning stock between area 2 and 3

and the observation that longer fish tend to have a more westerly starting point support the above theory. Which factor is the most important is most probably linked to the oceanographic conditions each year.

The estimation procedure

Two maturity stages are defined. All fish in stage M1 and higher will start the spawning migration early. All fish in stage M2 up to, but not including M1, will start the spawning migration late. A definition of "early" and "late" in terms of dates is immaterial here.

For each of the areas 5-8 and stages M1 and M2, a number P_j^i is defined. The upper index i takes the values 1 and 2 and designates the maturity stage. The lower index j takes the values 5-8 and designates origin area.

P_j^i yields the fraction of the fish migrating to area 3, $1-P_j^i$ yields the fraction of fish migrating to area 2. There exists 8 such numbers, the upper index designating the stage, the lower index designating area. Three simplifying assumptions have been made:

The most mature fish in area 5 will spawn in area 3, $P_5^1 = 1.0$.

The most mature fish in area 8 will spawn in area 3, $P_8^1 = 1.0$.

The least mature fish in area 6 will spawn in area 2, $P_6^2 = 0.0$.

The collection of P's will be called the migration pattern.

The components of the stock spawning in area 2 from each of the areas 5-8 were pooled together, and the mean length, L_2 calculated. The same was done for fish spawning in area 3. The mean length of the biological samples, l_2 , obtained for March was calculated. The goal function for the estimation is now defined as:

$$\sum_{\text{years}} ((L_2 - L_3) - (l_2 - l_3))^2$$

Thus, in order to estimate the migration pattern, the expression above is to be minimized.

Unknown factors

Maturity

We do not know specifically which maturity stage corresponds to fish that mature early, and which stage corresponds to fish maturing at all. The analysis is therefore carried out for two different cases:

- a) early migrating fish will be found in stage IIIa+ and late migrating fish will be found in stage IIb, and
- b) fish which migrate early will be found in stage IIIb+ and those which migrate late will be found in stage IIIa.

These stages are likely candidates for spring spawning (FORBERG and TJELMELAND, 1985).

Growth

By using length differences for comparison instead of absolute lengths, the uncertainty in the overall length growth during the period between the autumn and spring observations is removed. Still, the growth may have been different for fish in different geographical areas. Table 3 shows the otolith growth zone for the spring period for the fish that were used. The growth is more or less the same for fish found in area 2 and fish found in area 3. A slightly higher growth has, however, occurred for fish migrating to area 3 in 1985 and 1983. This difference in growth is corrected for by assuming a proportionality between the growth of otolith and the growth of length. The relationship of growth between length and otolith may not be the same for rapidly maturing fish as that of immature or slowly maturing fish. During the spawning migration, it is conceivable that excess energy is converted to spawning products rather than to growth in length. In this case the ratio of growth between length and otolith may be higher than average. Due to this consideration, the analysis has been performed for two cases. These are for full growth correction for 1983 and 1985, and half growth correction for 1983 and 1985.

Table 3. Spring otolith growth zone (mm) for 4 year old female capelin. Data from March samples.

Year	Area 2	Area 3
1981	0.047	0.044
1982	0.028	0.030
1983	0.024	0.038
1984	0.027	0.027
1985	0.038	0.063

During the autumn, there may be some growth between the time of measurement and the time of deposit of the winter ring. Table 4 shows the mean total otolith radius measured in the autumn and the mean total otolith radius measured during the spring. With correction for the spring otolith growth, it is seen that there was a non-negligible "rest autumn growth" during 1982 and 1985. With the method used in this paper, this can not be corrected for. If the rest autumn growth is much different for the different areas, our results become biased.

Table 4. Mean total otolith radii (mm).

	Autumn	Spring
1980-1981	0.897	0.947
1981-1982	0.907	0.978
1982-1983	0.909	0.948
1983-1984	0.916	0.946
1984-1985	0.904	0.970

ESTIMATION OF MIGRATION

Estimation of migration pattern for the years 1980-1985

Using the above outlined procedure, the migration pattern for the years 1980-1985 is estimated. The results are given in the text table below. Most later migrating fish (M2) from area 8 end in area 3. Most early migrating fish (M1) from area 7 end in area 3, most later migrating fish from area 7 end in area 2.

Migration pattern P_j^i 1980-1985

Full correction for 1983 and 1985 spring growth

	j	5	6	7	8
M1=IIIa	i=1	1.00	0.00	0.70	1.00
M2=IIb	i=2	0.94	0.00	0.01	0.73

M1=IIIa	i=1	1.00	0.02	0.79	1.00
M2=IIb	i=2	0.96	0.00	0.02	1.00

Half correction for 1983 and 1985 spring growth

	j	5	6	7	8
M1=IIIa	i=1	1.00	0.24	0.75	1.00
M2=IIb	i=2	1.00	0.00	0.13	0.74

M1=IIIa	i=1	1.00	0.00	0.73	1.00
M2=IIb	i=2	1.00	0.00	0.00	0.87

M2 is in both cases lower than M1 for area 7, in accordance with the migration theory.

Definition of the deviation from the migration pattern

The year-to-year deviation from the general migration pattern obtained above will be defined by a single parameter, D. This is added to P. The reasoning for this is that, if shifts in the ambient temperature cause a deviation from the general migration pattern, this deviation will be in the same direction for all areas, i.e. a cooling of the sea will lead to a more westerly spawning migration from all areas. By defining one single deviation parameter, the general trends for the impact of temperature on migration can be revealed. The influence of temperature may have a different magnitude for each area, but is not revealed by this procedure.

Confidence intervals

The variable

$$t = \frac{(L_2 - L_3) - (l_2 - l_3)}{\sqrt{\frac{1}{M} + \frac{1}{N}} \cdot s}$$

where M = Number of fish measured in area 2

N = Number of fish measured in area 3

$$s^2 = \left[\sum^M (l_{2_i} - l_2)^2 + \sum^N (l_{3_i} - l_3)^2 \right]$$

l_i is the individual length for the i -th fish

will have a t -distribution. This is used to construct 95% confidence intervals. In using this procedure, the number of measured fish is fixed. This simplification does not alter the confidence intervals very much, since the t -values corresponding to the confidence limits will not vary much when the number of observations is high. In all cases, there were so many observations that the asymptotical limit of a normal distribution nearly approximated.

Estimating deviation

Both combinations of estimating maturity stages (M_1 and M_2) give the same general result (Fig. 3).

During the period of autumn through spring, 1981/82, and 1982/83, the migration was more easterly than for that period of 1980/81. During this period for 1983/84, there was an abrupt shift to a westerly migration which reversed towards the average pattern during this period for 1984/85.

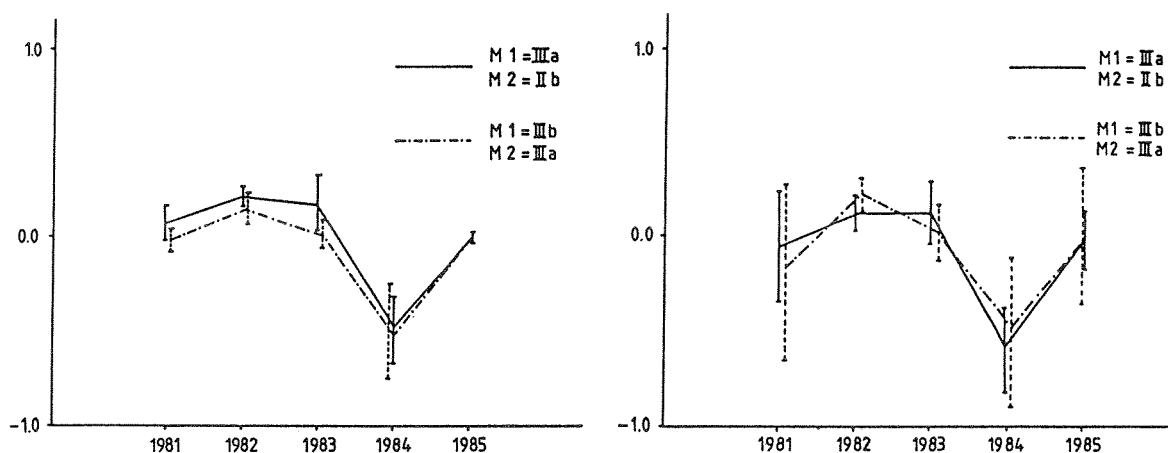


Fig. 3. Estimated migration deviation from the general migration pattern in Table 4. Left figure: Full correction of spring growth. Right figure: Half correction of spring growth.

These results have been obtained by relaxing the constraint of full migration to area 3 for the earliest migrating capelin from area 5 and 8, and full migration to area 2 of the latest migrating capelin from area 6. Estimates of migration with these constraints still in operation show nearly the same results with the exception of 1984, where the westwards migration has about half the value of the unconstrained case.

In some cases, the absolute value of migration (sum of P and D) is greater than one. However, the computer program forces all migration to lie in the range 0.0 - 1.0.

TEMPERATURE CHANGES 1980-1985

As an index for the temperature regime during the period, the temperature in

80-120 m depth in two locations near the coast, centered in area 2 and area 3 are (somewhat arbitrarily) chosen for the spring period, while the mean temperatures for the capelin distribution in areas 7 and 8 have been chosen for the autumn period. The latter figures are calculated by GJØSÆTER and LOENG (1987). The changes in temperature regime are given in Fig. 4.

There seems to be a general trend of increased temperatures during the spring. However, the most pronounced feature is the elevated temperatures for the eastern area during 1982 and 1983, which give rise to a vanishing, or negative, east-west gradient.

There also appears to be a general trend of increased temperatures during the autumn period. This is with the exception for 1984, when a cooling may begin. However, the trend is different for areas 7 and 8. The small decrease in temperature from 1980 to 1981 in area 8 gives rise to an increasing east-west gradient which later decreases until 1983. The east-west gradient again increases in 1984.

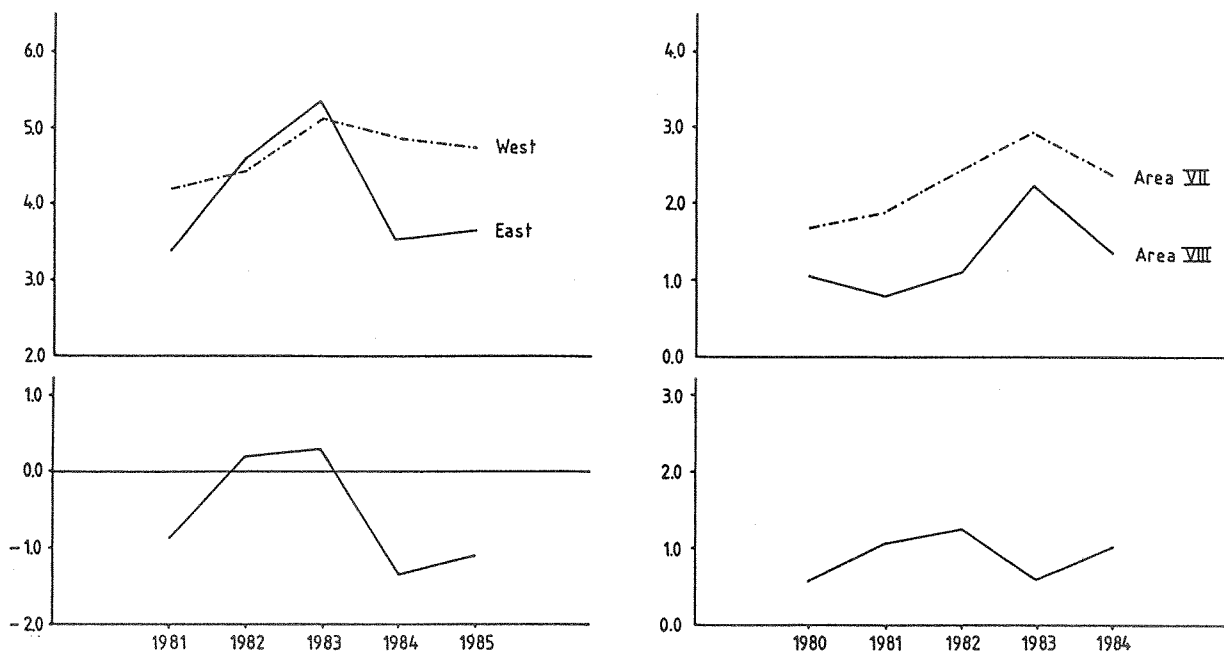


Fig. 4. Temperature indices for spring period (left) and autumn period (right). West-east gradient (spring) and east-west gradient (autumn) in bottom figure.

CONNECTION BETWEEN MIGRATION AND SEA TEMPERATURE

Temperatures in the spring period

The temporary shift in migration towards the west during 1982 and 1983 (spring) coincides with the heating of the coastal waters in 1982 and 1983. However, the temperature drop in 1984 was smaller than the westwards migration movement. Also, the eastwards displacement of migration in 1985 cannot be explained by the temperature level. The correspondence between migration and the east-west temperature gradient is better, such that high temperatures in the eastern part of the coastal area promoted an eastern migration. However, the great eastwards displacement during 1985 was not fully accounted for in this case either.

Temperature in the autumn period

There is a marked tendency to an anti-correlation between sea temperature in the autumn and migration deviation. The highest temperature reached during 1983 for both area 7 and 8 seems to correspond with the western maximum of migration. However, there is better correspondence between migration deviation and temperature gradient in this case, but the correspondence is to a positive, not a negative, gradient. This means that the migration would tend to be easterly if the temperature was much greater for the western than for the eastern part of the capelin distribution during the autumn.

Link between migration and temperatures

The estimations of migration made in this paper, together with the observed development of temperature during the autumn as well as spring, suggest that temperature gradients may be as important as the overall temperature level in the determination of the geographical distribution of the spawning migration. The positive correlation between east-west migration and the autumn temperature gradient is consistent with a theory that the capelin seeks cold temperatures during their pre-spawning migration, i.e. before the gonads are fully developed and some time before spawning. The negative correlation between east-west migration and the spring temperature gradient is consistent with a theory that the capelin seek a warm or some optimal temperature during the month prior to spawning.

The data used were not sufficient to decide which of these factors is the most important. Also, the data show a covariation between the gradients in the autumn and in the spring: High gradients in the autumn have occurred at the same time low gradients in the spring were measured. Therefore, a longer time series of data, where the reverse situation also occurs, is needed in order to quantify the two effects with respect to each other.

It is important to note that, in this context, the east- and westwards migration does not necessarily correlate well with a high abundance of mature capelin in the eastern and western regions of the spawning area, respectively. Our presentation demonstrates that there is a covariation between migration and temperature, irrespective of the actual distribution of the capelin during autumn. The abundance of mature capelin at the eastern and western parts of the spawning area will then be the combination of the migration and the geographical distribution during the onset of migration.

CONCLUSIONS

Although the link between temperature gradients and spawning migration has only been demonstrated for female 4 year old capelin (spring), there is reason to believe that the demonstrated method may be powerful in order to develop models of migration for the whole capelin stock.

A future development of the method would be to include more age groups and to allow the parameter of deviation to have different values in different areas. Also, we might use full distributions of length and distributions of age as comparative data. If so, however, problems concerning growth and the impact of the fishery will arise.

It is necessary to incorporate the geographical dimension and a submodel for migration into the present model for capelin in order to improve the base for

future management of the capelin stock. Furthermore, in order to take full advantage of the extensive scientific work on Barents Sea capelin and related subjects, a more comprehensive model of capelin is needed. The present paper is a first attempt to explore some of the possibilities and problems which advance a model for management through the construction of models for migration.

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