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The effect of temperature in the spawning and nursery areas on
recruitment of autumn-spawning herring in the North Sea

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1. Introduction

Year-class strength is considered to be largely dependent on the survival in the different stages of the life of the young herring, from the egg stage onwards. The factors governing this survival during the different stages of life may as well be biotic (predators, diseases, suitable food) as abiotic (temperature, salinity etc.). Within certain unknown limits recruitment strength seems not to be determined by the egg-production of the parent stock.

Blaxter and Hempel (1961) studied the success of the hatching and the survival of herring eggs and larvae under different controlled conditions. Blaxter (1956) showed (Figure 1) with eggs of autumn-spawning herring at temperatures ranging from 5.5° C to 14.5° C, a significant effect on the hatching success: at low temperatures the percentage hatched is significantly lower than at high temperatures. For spring-spawning herring Blaxter (1956) showed a highly significant negative relation between temperature and the hatching rate, within the same temperature range. The results of the experiments on the spring-spawning herring were confirmed by Hempel and Blaxter (1961) with eggs of continental spring-spawning herring (Kiel, Cuxhafen).

The experiments mentioned indicate that temperature conditions during spawning time on the spawning grounds may well be one of the factors directly controlling the success of recruitment.

This paper aims at investigating the relation between the spawning temperature and the subsequent recruitment of the autumn-spawning herring at the Doggerbank and in the Straits of Dover and English Channel. In addition, the effect of temperature conditions in the nursery areas on year-class strength of the mentioned populations has been studied. Moreover, the egg-production of the Dogger- and the Downs-stocks which might also affect year-class strength has been taken into account.

2. Material and methods

A. Recruitment data

The data of the Bank-stock (Table 1) are arrived at by analysis of the catch and catch-statistics of the Belgian and Dutch trawl fishery on spawning herring of the Doggerbank. The recruitment strength as at three years of age of the different year-classes, is calculated as the mean number of herring caught per day by a standard trawler of 500 B.H.P., using estimates of age-groups four and five only.

Table 1. Recruitment Dogger herring year-class 1947 - 1962

<u>Year-class</u>	<u>R3 x 1000</u>	<u>log.</u>	<u>Year-class</u>	<u>R3 x 1000</u>	<u>log.</u>
1947	14.6	2.16	1955	14.8	2.17
1948	7.0	1.85	1956	37.3	2.57
1949	11.7	2.07	1957	2.0	1.30
1950	5.9	1.77	1958	12.6	2.10
1951	6.7	1.83	1959	0.7	0.84
1952	23.5	2.37	1960	21.8	2.34
1953	4.3	1.63	1961	6.0	1.77
1954	6.3	1.33	1962	14.1	2.15

Year-classes 1947.- 1953 from Belgian trawl fishery.

Year-classes 1954 - 1962 from Dutch trawl fishery.

Data for the recruitment of the Downs-stock (Table 2) are derived from the routine sampling of drift-net caught herring in the southern North Sea (East-Anglia, Burd 1966). This herring is considered to be identical with the herring spawning on the grounds in the Straits of Dover and the English Channel.

Table 2. Recruitment Downs herring

<u>Year-class</u>	<u>R3 x 1000</u>	<u>log.</u>	<u>Year-class</u>	<u>R3 x 1000</u>	<u>log.</u>
1925	8.6	0.93	1945	40.9	1.61
1926	19.1	1.28	1946	44.3	1.65
1927	16.1	1.20	1947	22.6	1.35
1928	10.0	1.00	1948	25.5	1.41
1929	35.5	1.55	1949	26.8	1.43
1930	8.3	0.92	1950	31.5	1.50
1931	26.0	1.42	1951	21.8	1.34
1932	24.8	1.39	1952	10.9	1.04
1933	13.1	1.12	1953	32.1	1.51
1934	43.7	1.64	1954	24.3	1.39
1938	29.1	1.46	1955	9.5	0.98
1939	15.0	1.18	1956	18.0	1.26
1940	27.9	1.45	1957	3.0	0.90
1941	23.9	1.38	1958	36.6	1.56
1942	35.9	1.55	1959	3.0	0.48
1943	18.2	1.26	1960	18.0	1.26
1944	27.1	1.43	1961	16.8	1.23

B. Temperature data

Doggerbank (Table 3)

This set of data is arrived at from observations of bottom-temperatures by research vessel on the spawning grounds at 20 - 30 fathom depth, the places where the major spawning seems to occur in the second half of September. Additional data are derived from the I.C.E.S. Hydrographical Bulletins.

Table 3. Bottom temperatures on the Doggerbank, 20 - 30 fathoms. 2nd half of September.

<u>Year</u>	<u>t°C</u>	<u>Year</u>	<u>t°C</u>
1947	(13.5)	1954	12.4
1948	(14.0)	1955	12.3
1949	(13.2)	1956	12.0
1950	(13.1)	1957	13.1
1951	(12.8)	1958	12.4
1952	(12.9)	1959	15.4
1953	(13.6)	1960	12.0
		1961	14.5
		1962	13.3

The temperature data in paranthese are based on less than three observations.

Sandettie - Channel (Table 4)

A complete set of data of bottom-temperatures on the different spawning places in the southern North Sea and English Channel was not available. As representative for the temperature conditions on the spawning grounds in December, the surface temperature in December is chosen on the position of the North-Hinder lightvessel (51°39' N.L. - 2°34' E.L.).

It is, however, realized that direct observations during the spawning time on the spawning grounds proper are far more desirable.

Table 4. Surface temperature in December on the position 51°39' N.L., 2°34' E.L. of the North Hinder lightvessel.

<u>Year</u>	<u>t°C</u>	<u>Year</u>	<u>t°C</u>
1925	7.3	1944	(9.8)
1926	8.7	1945	(9.2)
1928	9.8	1946	(9.0)
1929	10.5	1947	(10.5)
1930	9.9	1948	9.9
1931	8.3	1949	10.3
1932	8.7	1950	9.0
1933	7.6	1951	11.0
1934	11.0	1952	8.7
1935	9.0	1953	11.2
1936	9.1	1954	10.7
1937	9.5	1955	9.6
1938	10.0	1956	9.2
1939	(9.6)	1957	9.2
1940	(9.7)	1958	10.0
1941	(9.7)	1959	11.0
1942	(10.4)	1960	10.4
1943	(9.6)	1961	9.3

The data are the monthly means of the daily observations. The data in parentheses are calculated by the regression between the air temperature in Den Helder and the North Hinder sea-temperature.

Nursery areas (Tables 5 and 6)

As representative for the temperature conditions in the nursery areas in the spring and summer months, the observations of the surface temperature in April and June on the position of lightvessel Texel (53°02' N.L. - 4°22' E.L.) and April and August of the Vyl lightvessel (55°24' N.L. - 7°34' E.L.) have been chosen.

Table 5. Surface temperature in April and June on the position 53°02' N.L., 4°22' E.L., of the Texel lightvessel.

<u>Year</u>	<u>April</u>	<u>June</u>	<u>Year</u>	<u>April</u>	<u>June</u>
1925	7.3	13.4	1946	7.1	13.5
1926	8.4	13.2	1947	5.6	15.6
1927	8.3	12.7	1948	8.1	14.4
1928	7.4	12.6	1949	7.6	13.5
1929	4.9	12.0	1950	7.8	14.8
1930	7.2	13.7	1951	6.7	13.4
1931	6.3	12.1	1952	6.7	13.9
1932	6.6	12.9	1953	6.6	13.5
1933	7.6	13.8	1954	6.0	13.5
1934	5.6	12.9	1955	5.0	11.4
1935	7.2	13.2	1956	5.3	12.2
1936	7.1	13.4	1957	8.6	13.7
1937	7.3	13.9	1958	5.1	12.5
1938	7.5	13.0	1959	7.8	14.1
1939	7.6	13.8	1960	6.9	13.6
1940	6.4	14.4	1961	8.5	14.0
1941	5.9	13.0	1962	5.7	11.9
1942	5.6	12.9	1963	4.1	12.4
1943	8.5	14.3	1964	5.3	13.4
1944	4.9	12.8	1965	6.6	12.3
1945	8.7	14.8	1966	6.6	13.7

The temperature is the monthly mean of the daily observations. The data in parentheses are calculated by the regression between the air-temperature in Den Helder and the sea-surface temperature at Texel lightvessel.

Table 6. Surface temperature in April and June on the position 55°24' N.L., 7°34' E.L. of the Vyl lightvessel.

<u>Year</u>	<u>April</u>	<u>August</u>	<u>Year</u>	<u>April</u>	<u>August</u>
1946	4.7	16.6	1957	6.6	16.0
1947	1.0	18.1	1958	2.9	16.3
1948	7.0	16.7	1959	6.2	18.1
1949	5.5	15.4	1960	4.8	16.2
1950	6.2	17.5	1961	7.1	15.6
1951	5.0	16.3	1962	4.8	15.3
1952	4.7	16.3	1963	3.1	16.4
1953	5.7	16.7	1964	3.6	15.7
1954	4.2	15.6	1965	4.7	15.8
1955	3.5	17.1	1966	3.9	15.9
1956	3.5	15.0			

The data are published in the "Annales Biologiques" by H. Thomsen (Denmark).

C. Correlation

Recruitment data of the two stocks have been correlated with temperature conditions during the incubation time of the eggs on the spawning grounds, and with the temperature conditions during the spring and autumn (in the nurseries) during the first year of life. When possible partial and multiple correlation coefficients between recruitment and two factors were determined. Recruitment data have been log-transformed to get normal distributions.

3. Results

A. Correlations recruitment Dogger (Table 7)

The temperature and recruitment data for 1954 - 1962 are the most reliable, being based on nurseries observations. It is apparent that recruitment and spawning temperature are correlated negatively, both single (r.01) and partial correlations (r.01/2, r.01/3, r.01/4, r.01/5) are significant.

Of the single and partial correlations between recruitment and temperature in the nurseries, only those between recruitment - April temperature Vyl (r.04) and the recruitment - April temperature Vyl excluding the August temperature (r.04/5) are nearly significant.

The multiple correlations between recruitment - spawning temperature + temperature nursery are all significant; it should be noted that the relation recruitment - spawning temperature + April temperature Vyl (r.0.14) is the highest.

The 1946 - 1962 set of data is merely used to confirm the phenomena apparent in the 1954 - 1962 data. The same correlations appeared to be significant but in addition the partial correlations between recruitment April temperature Texel, without the effect of June temperature Texel (r.02/3) and recruitment - April temperature Vyl, without the influence of Vyl temperature August (r.04/5), were both positive and significant.

It may be concluded from these data that the recruitment strength of the herring spawning at the Doggerbank is largely determined by the temperature conditions during the spawning time in September on the spawning grounds and by the temperature conditions prevailing in the nurseries in the first year of life, in April.

Relatively low temperatures in September on the spawning positions, and relatively high temperatures in April in the nursery areas are in favour of a good recruitment of the Dogger herring.

Table 7. Correlations recruitment Dogger 1947 - 1961, 1954 - 1962.

<u>Single</u>	<u>1947-1961</u>	<u>sign</u>	<u>1954-1962</u>	<u>sign</u>
r.01 =	-0.7335	xxx	-0.7719	xxx
r.02 =	+0.4801	---	+0.2755	---
r.03 =	+0.2397	---	+0.1339	---
r.04 =	+0.5929	x	+0.5535	---
r.05 =	+0.0760	---	-0.0572	---
<u>Partial</u>				
r.01/2 =	-0.7568	xxx	-0.7544	x
r.01/3 =	-0.7544	xxx	-0.7673	x
r.01/4 =	-0.8092	xxx	-0.8522	xxx
r.01/5 =	-0.7350	xxx	-0.7961	x
r.02/1 =	+0.5369	x	+0.1228	---
r.02/3 =	+0.5374	x	+0.3135	---
r.03/1 =	+0.3477	---	+0.0234	---
r.03/2 =	-0.3500	---	-0.1078	---
r.04/1 =	+0.7180	xxx	+0.6371	---
r.04/5 =	+0.5942	x	+0.5625	---
r.05/1 =	-0.1041	---	-0.3116	---
r.05/4 =	-0.1051	---	-0.1323	---
<u>Multiple</u>				
r.0.12 =	0.8209	xxx	0.7759	x
r.0.13 =	0.7706	xxx	0.7720	x
r.0.14 =	0.8803	xxx	0.9000	xxx
r.0.15 =	0.7369	xxx	0.7764	xxx

Table continued...

Table 7 (cont.)

<u>Serie</u>	<u>n</u>	<u>significance</u>	<u>df</u>	<u>5 % (x)</u>	<u>1 % (xx)</u>
1947-1961	15		14	0.4770	0.6230
1954-1962	9		13	0.5140	0.6410
			8	0.6320	0.7650
			7	0.6660	0.7980

0 = recruitment, 1 = spawning temperature, 2 = April temperature Texel, 3 = June temperature Texel, 4 = April temperature Vyl, 5 = August temperature Vyl.

B. Correlations recruitment Downs herring (Table 3)

The set of temperature and recruitment data from 1925 until 1961 can be divided in pre-war (1925-1939) and post-war material (1946-1961). Of the single correlations in the 1926-1939 set only the correlation recruitment - June temperature Texel (r.03) is significant and the positive relation recruitment - December temperature H.Hinder (r.01) is nearly significant.

Of the partial correlations, the relation recruitment - June temperature excluding the effect of the December temperature (r.03/1) and the relation recruitment - spawning temperature without the influence of the April temperature (r.01/2) are both significant and positive. The latter is caused by a negative correlation between the December temperature ant H. Hinder and the April temperature in the following year at Texel lightvessel. The multiple correlations between recruitment-spawning temperature and April temperature Texel (r.0.12) and recruitment-spawning temperature + June temperature Texel (r.0.13) are both significant. The 1925 - 1961 data largely confirm the relations found in the 1925 - 1939 set of data. The partial correlation between recruitment - April temperature, eliminating the influence of the December temperature (r.02/1) has become highly significant.

The data for 1946 - 1961, however, do not show any of the herefore mentioned relations.

From the Downs data we may conclude that recruitment of this population before 1940 was influenced by the temperature conditions on the spawning grounds and by the temperature conditions in spring and pre-summer in the nursery areas during the first year of life. Relatively high temperatures in both the spawning and nursery areas were in favour of a successful recruitment.

The inverse relation between the December H. Hinder temperature and the April temperature at Texel masked the effect of the spawning temperatures on recruitment.

The failure of the correlations after 1946 will be discussed in the next chapter.

Table 3. Correlations recruitment Downs 1925 - 1939, 1946 - 1961, 1925 - 1961.

<u>Single</u>	<u>1925-1939</u>	<u>sign</u>	<u>1946-1961</u>	<u>sign</u>	<u>1925-1961</u>	<u>sign</u>
r.01 =	+0.4788	---	+0.0455	---	+0.2941	---
r.02 =	+0.2996	---	+0.1819	---	+0.2641	---
r.03 =	+0.5239	x	+0.3650	---	+0.4429	x
<u>Partial</u>						
r.01/2 =	+0.5649	x	+0.0550	---	+0.4994	xx
r.01/3 =	+0.4761	---	-0.0430	---	+0.1572	---
r.02/1 =	+0.4425	---	+0.1874	---	+0.4833	xxx
r.02/3 =	+0.1199	---	+0.3446	---	+0.1266	---
r.03/1 =	+0.5266	x	+0.3647	---	+0.3766	xx
r.03/2 =	+0.4600	---	+0.1302	---	+0.3392	x
<u>Multiple</u>						
r.0.12 =	0.6166	x	0.1898	---	0.5476	xxx
r.0.13 =	0.6654	xxx	0.3673	---	0.4600	x

Table 3 (cont.)

<u>Serie</u>	<u>n</u>		
1925-1939	16		
1946-1961	12		
1925-1961	28		
Significance d.f		5 %	
		x	xx
	27	0.3670	0.4700
	26	0.3740	0.4730
	15	0.4820	0.6060
	14	0.4970	0.6230
	11	0.5520	0.6840
	10	0.5760	0.7030

0 = recruitment, 1 = December temperature H. Hinder, 2 = April temperature Texel, 3 = June temperature Texel.

4. Discussion

A. Recruitment - spawning temperature

In the introduction the experiments of Blaxter and Hempel on hatching success of eggs of autumn- and spring-spawning herring at different incubation temperatures are mentioned. These experiments revealed a correlation between the incubation temperature and the proportion hatched; the correlation was positive in the case of the eggs of autumn-spawning herring and negative for the eggs of spring-spawning herring. Blaxter suggested that the difference in sign of the relations might be caused by hereditary factors. Willemsen (1953) found in the experiments with eggs of Esox lucius on the survival of these eggs until the larval stage at different incubation temperatures an optimum shaped curve, with an optimum survival of 50 % between 8° and 12° C.

It is possible that the relation between the incubation temperature and the survival of the herring egg until the larval stage might be fitted by an optimum curve. The position of the optimum temperature and not the sign of the correlation might be the difference between the relation temperature-hatching success of autumn- and spring-spawning herring (Figure 1). In the light of Blaxter's and Willemsen's experiments the negative and positive correlation between recruitment and spawning temperature resp. the Dogger- and Downs-population can be understood. The regressions of both correlations may each be a part of an optimum curve with the optimum at the 12° C.

Temperatures in the second half of September on the Doggerbank, at a depth of 20 - 30 fathoms, are varying between ± 12° - 15° C; in December the surface temperatures at the position of H. Hinder lightvessel are ranging from 7° - 11° C. The relationship between year-class strength and spawning temperature failed in the Downs area after 1946. The cause for this can be twofold.

- (a) An increase of the December temperature at the H. Hinder lightvessel in the years 1946 - 1961 as compared with the years 1925 - 1940. In the years 1925 - 1940 temperatures ranged from 7.3 to 11.0°C, with only three years with temperatures over 10° C. In the years 1946 - 1961 temperatures ranged from 8.7 - 11.2 C, with eight years with temperatures over the 10° C. When the real relation between recruitment and spawning temperature can be described by an optimum curve, with an optimum around 12° C, the possibility to find a significant correlation decreases when the temperatures get closer to the optimum situation. This also means that during this period recruitment was more or less independent of spawning temperature and in the optimum position for recruitment.

- (b) A decrease of the egg-production of the Downs population after 1955. This will be discussed in the next paragraph.

B. Recruitment - egg-production

Studying the causes of the fluctuations in year-class strength, the effect of egg-production upon recruitment has to be taken into account. The spawning potential of the stock will be used in this paragraph as the egg-production of the stock, as there are no methods to measure the egg-production of a herring population directly, except of those populations which spawn in intertidal zones (British Columbia). The egg-production of the Dogger- and Downs-populations are given in Tables 9 and 10, for the years 1946 - 1961. In both series a decline of the egg-production is apparent. Data on egg-production are relative and cannot be compared with each other.

Table 9. Egg-production Dogger population 1946 - 1967.

<u>Year</u>	<u>Numbers</u> <u>x 10</u>	<u>year</u>	<u>Numbers</u> <u>x 10</u>
1946	3.27	1956	2.04
1947	1.84	1957	1.68
1948	1.29	1958	1.63
1949	2.16	1959	1.49
1950	2.25	1960	1.66
1951	1.33	1961	1.11
1952	2.02	1962	0.63
1953	1.96	1963	1.55
1954	1.75	1964	1.11
1955	1.92	1965	0.89
		1966	0.74
		1967	0.63

The egg-production of the Dogger herring population is calculated by raising the numbers of herring in the length distribution of the daily catch of a trawler of 500 B.H.P. with the numbers of eggs produced by herring of different lengths (Zijlstra, 1963).

Table 10. Egg-production Downs population 1946 - 1961.

<u>Year</u>	<u>Numbers x 10⁹</u>	<u>Year</u>	<u>Numbers x 10⁹</u>
1946	1.70	1954	1.42
1947	1.71	1955	1.32
1948	1.62	1956	0.96
1949	1.62	1957	0.32
1950	1.70	1958	0.63
1951	1.65	1959	0.53
1952	1.64	1960	0.92
1953	1.61	1961	1.36

The 1946 - 1956 data (English) and the 1956 - 1961 data (Dutch) are based on the numbers of herring per shot (not corrected for efficiency) raised with the numbers of eggs produced by herring of different lengths.

Correlation calculations between recruitment and egg-production were carried out for both stocks, the data are given in Tables 11 and 12.

Dogger population (Table 11)

The egg-production seems to have no influence on the success of the subsequent recruitment ($r_{06} = +0.1335$), even if the effect of spawning temperature is eliminated ($r_{06/1} = -0.1543$). On the other hand, the number of eggs spawned seems not to interfere with the relation spawning temperature/recruitment success ($r_{01/6} = -0.7335$).

Table 11. Correlations egg-production Dogger herring 1947 - 1962.

<u>Single</u>	<u>1947-1962</u>	<u>sign</u>
r.01 =	-0.7335	---
r.06 =	+0.1335	---
<u>Partial</u>		
r.01/6 =	-0.7335	---
r.06/1 =	+0.1543	---
<u>Multiple</u>		
r.0.16 =	0.7400	---
n = 16	sign.	d.f.
		5%
		1%
		0.4820
		0.6060
		0.4970
		0.6230

0 = recruitment, 1 = spawning temperature Dogger, 6 = egg-production Dogger herring.

Downs population (Table 12)

The correlation between recruitment success and egg-production is nearly significant (r.04 = +0.4511), and when the effect of the April temperature Texel is eliminated it becomes significant (r.04/2 = +0.5315). The combined influence of the egg-production + April temperature nursery (r.0.24 = 0.5511) and the egg-production + June temperature nursery (r.34 = 0.5031) year-class strength are both significant.

From these data it may be concluded that in the period 1946 - 1961 the recruitment of the Downs stock was related to the egg-production and consequently the drop in the recruitment of the Downs herring can be related to the decrease of the egg-production of this stock.

When the effect of egg-production was eliminated, still no relation could be shown between temperature on the spawning grounds or in the nursery in April and June.

It must be stressed that the variation in the egg-production of the Downs stock of herring during 1946 - 1961 was considerably larger than that in the Dogger population (Tables 9 and 10).

Table 12. Correlations egg-production Downs herring 1946 - 1961.

<u>Single</u>	<u>1946-1961</u>	<u>sign</u>
r.01 =	+0.0455	---
r.02 =	+0.1319	---
r.03 =	+0.3650	---
r.04 =	+0.4511	---
<u>Partial</u>		
r.01/4 =	+0.0610	---
r.02/4 =	+0.2283	---
r.03/4 =	+0.2614	---
r.04/1 =	+0.4525	---
r.04/2 =	+0.5315	---
r.04/3 =	+0.3793	---
<u>Multiple</u>		
r.0.14 =	0.4544	---
r.0.24 =	0.5511	---
r.0.34 =	0.5031	---

Table 12 (cont.)

n = 16	sign.	d.f.	5%	1%
		15	0.4820	0.6060
		14	0.4970	0.6230

0 = recruitment, 1 = December temperature N. Hinder, 2 = April temperature Texel, 3 = June temperature Texel, 4 = egg-production Downs herring.

C. Recruitment - temperature nursery

The factor "temperature nursery", which is found to be related to recruitment strength, is chosen as an exponent of the general living conditions of the young herring in the nursery areas. The production cycle in sea is apt to start earlier in years with high values of sun radiation and sea-water temperatures, which are affecting the feeding conditions of the young herring. Roughly speaking high sea-water temperatures are likely to represent good and low temperatures poor feeding conditions.

Bückmann (1950) has shown that herring larvae from the central and southern North Sea are transported to the continental coast (Holland, Germany and Denmark) and invade the estuaries and other inlets from February until April. Recent Dutch investigations in 1967 and 1968 on the immigration of herring larvae in the Dutch Waddensea confirmed the German observations.

Dogger population

The temperature conditions in spring on the Dutch coast (Texel) and the Danish coast (Vyl) could be related with year-class strength, whereas the summer conditions seemed to have less influence. Possibly by that time the immature herring from the central North Sea are already leaving the coastal areas.

Downs population

The year-class strength of the Downs population is, according to the 1925 - 1961 data, influenced by the spring- and summer-temperature conditions on the continental coast (April and June, Texel). This could be tentatively explained in terms of a longer presence of young herring in the coastal areas compared with the young herring in the central North Sea.

D. General

In the preceding chapters it is shown that temperature conditions both on spawning grounds and in the nurseries influence are connected with factors influencing year-class strength of North Sea autumn-spawning herring.

It might be expected, therefore, that long-term fluctuations in the temperature conditions have an effect on the abundance of the herring stocks in the North Sea, as has been suggested by Bogdanov and Fedorov (1965) for the Atlanto-Scandian herring.

Downs population

For the Downs population the overall increase in temperature in the spawning area since 1922 (Figure 2) should have been favourable, since 1933 temperatures are over normal and during the period 1946 - 1952 they are extremely favourable. In the sixties, however, spawning temperature show a tendency to decline again. Temperature conditions in the nursery areas, especially in June, were also improving since 1922 and followed more or less the same trend as the December temperatures. The spring temperatures fluctuated a good deal, but after 1946 they follow the same pattern as the June temperatures and show a tendency to decline since 1952 (Figure 2).

However, the possibility to compare the overall stock density with natural conditions is seriously hampered by human interference through its fisheries; but it seems very likely that the Downs stock has built up itself during the thirties and forties, favoured by natural conditions and the fishery-stop during the second world war.

After 1946 natural conditions remained favourable, but attracted by the enormous abundance of the herring in southern North Sea a heavy fishery developed, yielding substantial catches and consequently causing a heavy mortality in the end.

So it looks as if since the fifties the Downs stock has run a double hazard resulting in very low abundances. Temperature conditions in the nurseries worsened in the fifties, followed by the temperature conditions on the spawning grounds in the sixties. The heavy fishery caused a depletion of the parent stock, and consequently a decline in egg-production and, as shown above, this could be correlated with poor recruitment.

Dogger population

The Dogger material only covers the period after 1946. The spawning temperatures since 1946 were decreasing slowly and getting more favourable for good recruitment (Table 3). After 1956, two for the Dogger very warm years, 1959 and 1961 followed, with a very cold year (1960) in between. Conditions in the nurseries were, as for the Downs stock, favourable in the forties but became poorer in the fifties, with some warm years 1957, 1959 and 1961.

The Dogger population is like the Downs stock heavily fished at present, with rising mortalities and a decreasing egg-production but until 1961 no relation between egg-production and recruitment could be shown. However, since 1961 egg-production has steeply declined in the Dogger area (Table 9). The recent low egg-production figures have not been incorporated in the calculations in this paper, as the resulting year-class strength is not yet fully known.

5. Conclusions

- (a) Temperature conditions on the spawning grounds of autumn-spawning North Sea herring during incubation time seem to affect year-class strength possibly through the differential egg-mortality at different temperatures.
- (b) There are indications that the relation between year-class strength and spawning temperature is fitted by a dome-shaped curve, with optimum conditions around 12° C.
- (c) The experiments of Blaxter (1956) on the differential hatching success at different incubation temperatures for autumn-spawning herring tend to confirm the suggestion under (b).
- (d) Higher temperatures in the coastal nurseries for half a year old herring in spring and pre-summer are favourable (or are connected with favourable conditions) for the autumn-spawning North Sea herring.
- (e) The egg-production of the Downs population after 1946 could be related to the recruitment of this stock, which was not possible for the Dogger population. The variation in egg-production in the Downs stock in the period studied, however, was larger than that of the Dogger stock.

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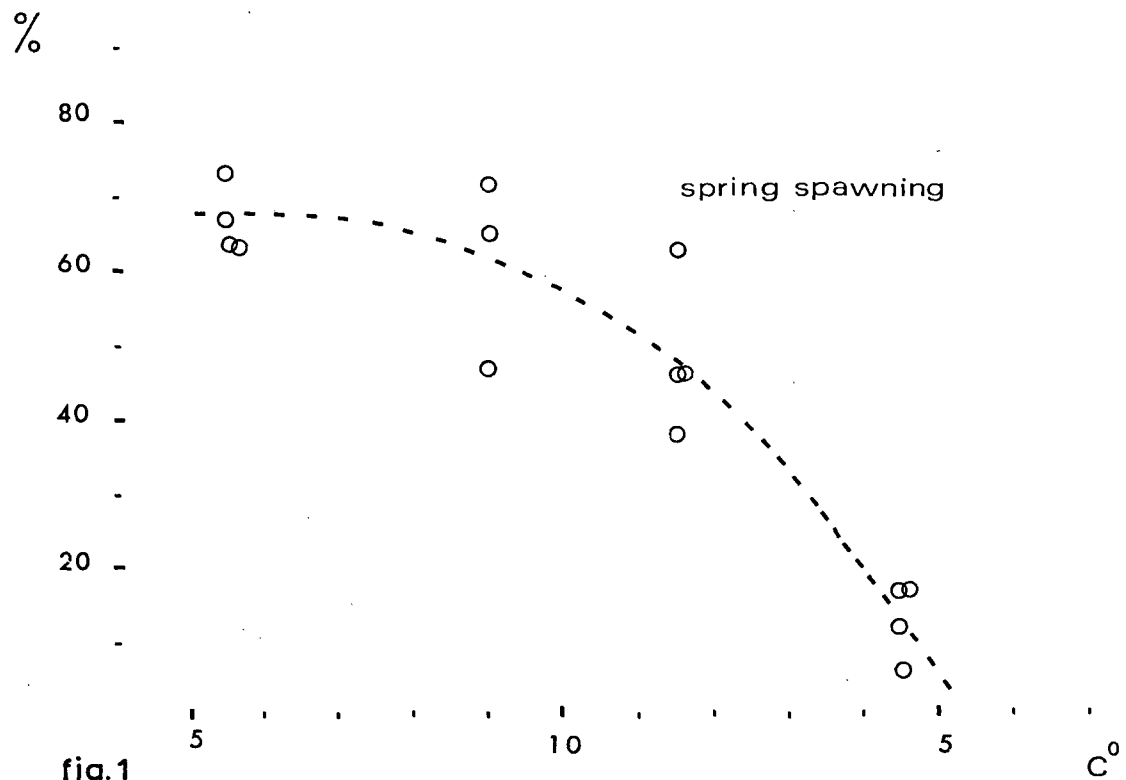
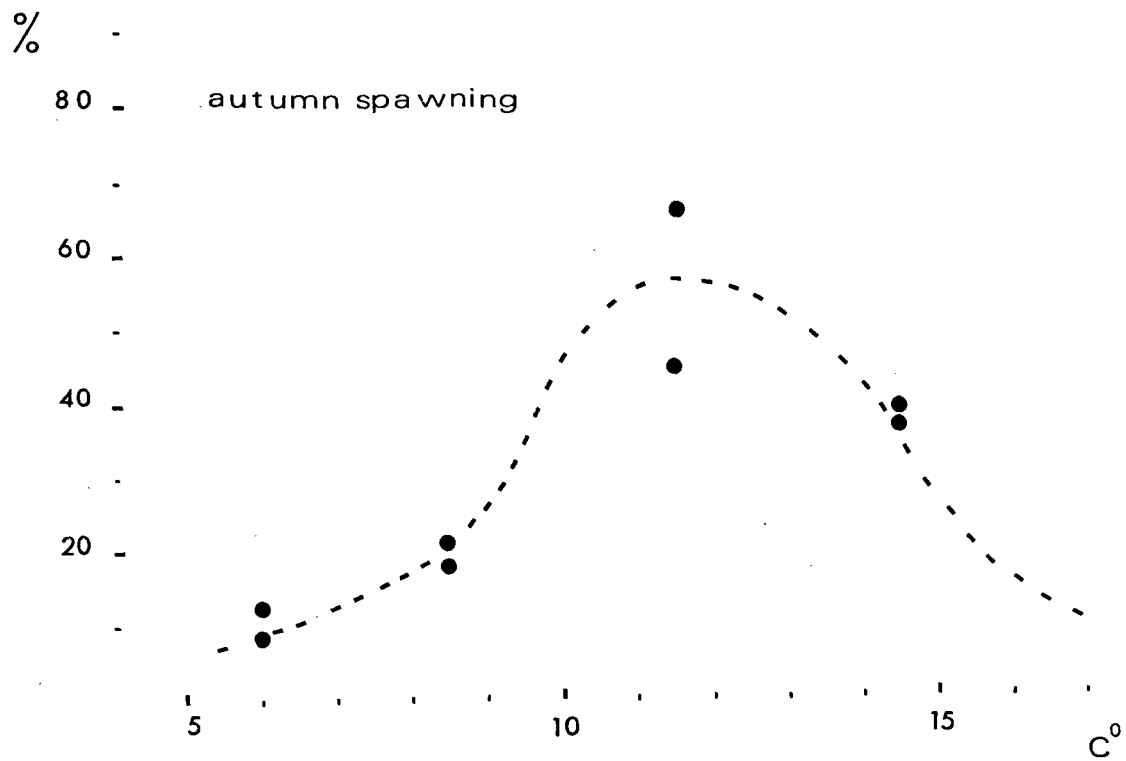


fig.1
 The hatching percentage on gauze at different incubation temperatures of eggs of autumn- and spring spawning herring (Blaxter 1956).

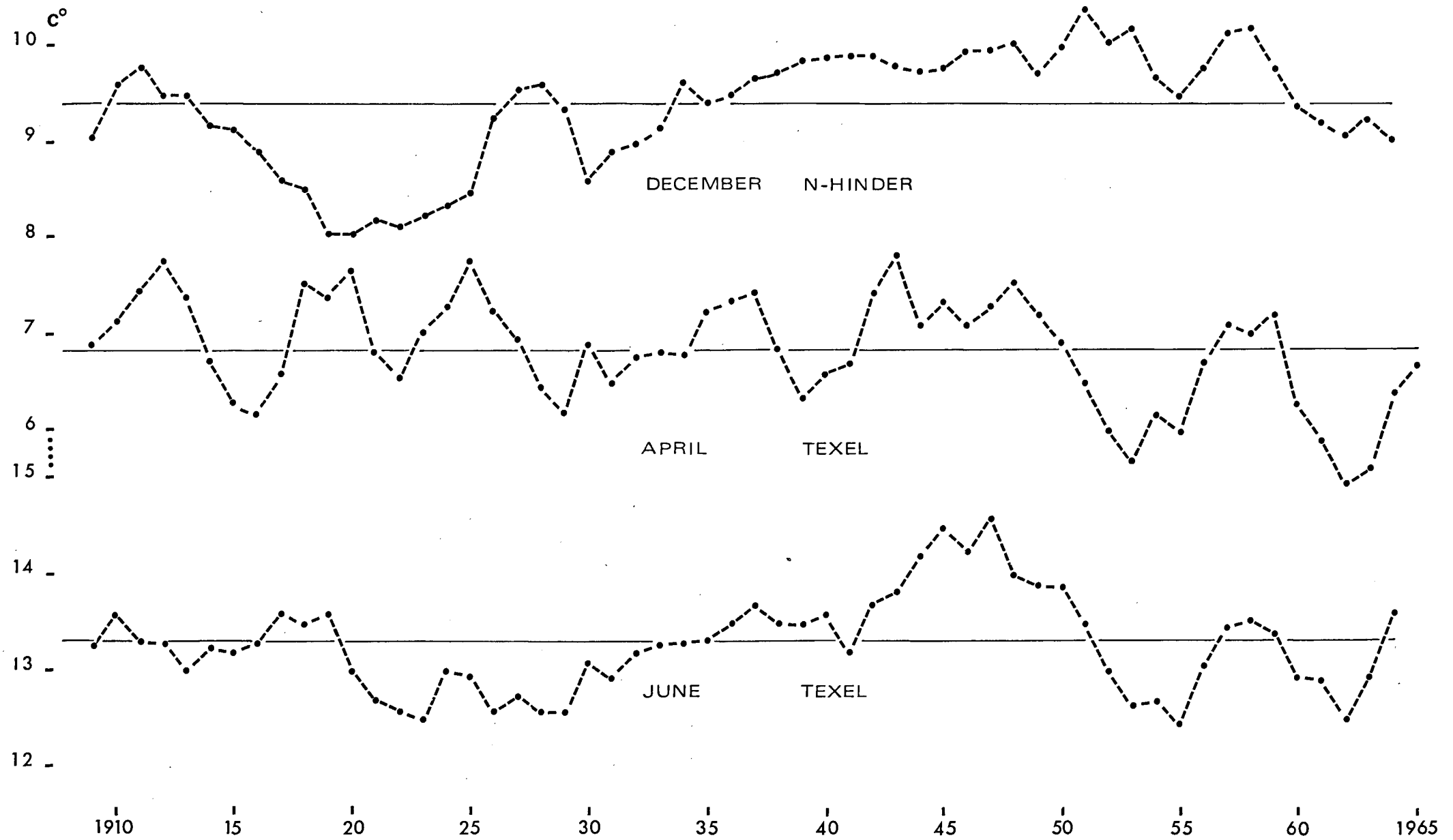


fig.2 Four year running mean of the surface seawater temperature at the position of the lightvessels N.Hinder and Texel.