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FACTORS INFLUENCING YEAR-CLASS STRENGTH OF NORWEGIAN SPRING SPAWNING HERRING
(*Clupea harengus* Linné)

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INTRODUCTION

Short and long term variations in abundance of recruits in the Norwegian spring spawning stock of herring (subsequently referred to as Norwegian herring) have been described by several authors (HJORT 1914, LEA 1930, DEVOLD 1963, MARTI and FEDOROV 1963). MARTI (1959) compared the relative strengths of poor and rich year-classes of herring in different areas. For Baltic herring he found a ratio of 1/2–1/3, for North Sea herring, 1/8–1/10 and for Atlanto-Scandian herring, to which the Norwegian herring belong, 1/25–1/30. LEA (1930) estimated the ratio between poor and rich year-classes (with reference to the rich 1904 year-class) in the Norwegian herring stock to be about 1/94. ØSTVEDT (1963) found a ratio of 1/15 for the 1949–1950 year-classes. Thus year-class fluctuations are more pronounced for Norwegian herring than for many other herring stocks in the Northeast Atlantic. Also the time interval between the appearance of rich year-classes can be relatively long, in some periods even more than ten years (LEA 1930, MARTI and FEDOROV 1963).

The variation in year-class strength in marine fishes is a general phenomenon. The causes of the variation are not known, but the current hypotheses concentrate on possible variability of parental factors (MARTI 1959, BRIDGER 1960, 1961, CUSHING and BRIDGER 1964, CUSHING 1968) and of physical and biological conditions in the sea shortly after hatching (HJORT 1914, 1926, ROLLEFSEN 1930, LEA 1930, WALFORD 1938, 1946, SETTE 1943, CARRUTHERS *et al.* 1951, WIBORG 1957). A marked relationship between the number of eggs produced (the spawning potential of the parent stock) and the number of subsequent recruits is demonstrated for some species of fish with low fecundity, e.g. spurdog (*Squalus acanthias* Linné) (HOLDEN 1968). Similarly an indication of such a relationship is found in some relatively small stocks of Pacific herring (*Clupea pallasii* Valenciennes) in British Columbia (TAYLOR 1963) and in the Downs stock of herring in the North Sea (BURD and HOLFORD 1968), but no trend of decreasing recruitment with decreasing spawning stock has as yet been demonstrated for the other major stocks of herring in the North Sea (the Buchan and the Bank stocks) and in the Norwegian Sea (the Norwegian herring). However, within the range of population sizes for which data have been available for these stocks, a relationship between the spawning potential of the parent stock and the subsequent year-class strength is difficult to trace due to the variations in the normally high natural mortality rate of the very young stages. Most of the newly hatched larvae die, and slight changes in the mortality rate in the young stages will therefore result in pronounced variations in year-class strength.

Little is known about the causes of the natural mortality rate of the young stages of fish and whether or not there exist periods when the mortality rate is exceptionally high. HJORT (1914, 1926) expounded the concept of a critical period at the end of the yolk sac stage when the larvae begin feeding. Experiments carried out on herring (SOLEIM 1942) indicated that a critical period existed at this stage. Thus the natural conditions during the early stages of the life might determine the abundance of herring entering the exploited stock and the variations in spawning potential and its influence on subsequent year-class strength might be of minor importance when the size of the spawning stock is above a certain level.

In view of the serious decline in the yield of adult Norwegian herring during the late 1950s and early 1960s the Herring Committee of the International Council for the Exploration of the Sea (ICES) recommended that special attention should be given to the recruitment problem in this stock (PARRISH 1963). At the Institute of Marine Research, Bergen, investigations of the variation in size of the spawning stock, the location and time of spawning, the identification of possible critical stages during the early larval development and the larval drift have been emphasized. During the same period extensive investigations were conducted to register the distribution, migration, abundance and mortality of young and adolescent herring. The results of the latter investigations are presented in a separate paper (DRAGESUND 1970) while this account is confined to:

1) spawning characteristics, i.e. the structure and size of the spawning stock and the location and time of spawning;
2) larval studies during the first month after hatching.

The discussion is centred on year-class fluctuations in relation to spawning characteristics and to environmental conditions during the egg stage and early larval development.

MATERIAL AND METHODS

The major part of the material is related to the 1959–1965 year-classes, and the data are mainly obtained from:

1) samples of herring collected during the Norwegian winter herring fisheries in 1959–1968;
2) tagging experiments carried out in 1952–1964;
3) samples of herring larvae collected in 1959–1965 and in 1968;
4) larval drift experiments;
5) official fishery statistics and meteorological annals.

When it is of importance to extend the information to other year-classes, data from the literature and unpublished data from the records of the Institute of Marine Research, Bergen, are used.

The statistical methods applied are those given in text books of statistical analysis (SNEDECOR 1956, GODSKE 1966). Geographical names or area code numbers used in the text are shown in Fig. 1. The hydrographical data are from the records of the Institute of Marine Research, Bergen.

ADULT HERRING

Samples of adult herring, each usually consisting of 100 specimens, were collected from commercial catches several times each week during the Norwegian winter herring fishery. Fresh or iced material was brought to the laboratory for examination. Until January 1963 lengths were measured to the nearest half cm and after this date to the half cm below as recommended by ICES (ANON. 1963). To make the data comparable a correction factor of 0.25 cm has been added to the mean lengths of herring in samples collected after January 1963. Ages were determined from scale readings. The weight in g was recorded, and the maturity stages were classified according to the scale recommended by ICES (ANON. 1963). This maturity scale comprises eight stages including six which describe the sexual cycle of adult fish, i.e. stages III–VIII. The stages V–VII represent the pre-spawning, the spawning and the spent phases, respectively.

Stage V. Gonads fill body cavity. Eggs large, round, some are transparent. Ovaries yellowish, testes milk white. Sperm does not flow, but can be extruded by pressure.

Stage VI. Eggs transparent. Testes white. Eggs and sperm flow freely.

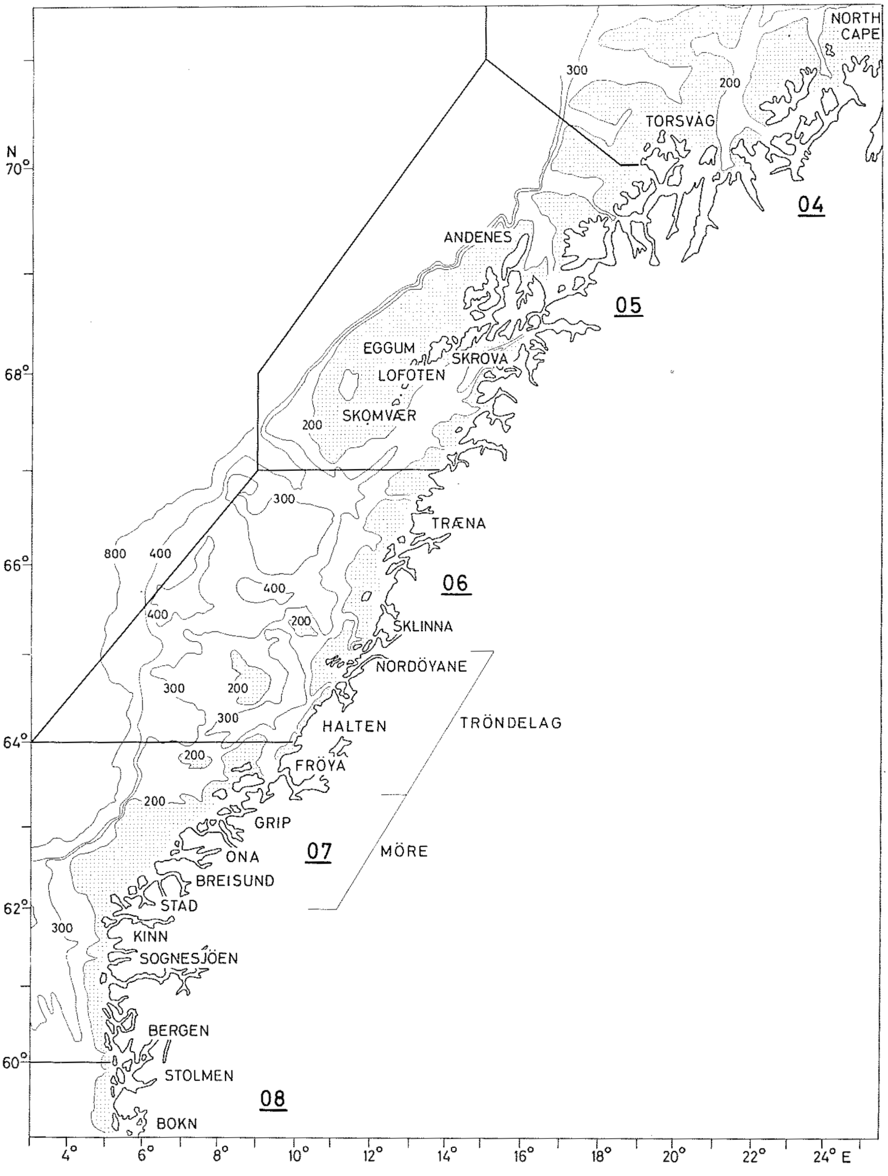

Fig. 1. Names and code numbers of areas mentioned in the text, and general bathymetric features of the coastal banks (depths in m).

Stage VII. Gonads baggy, bloodshot. The ovaries empty or containing only a few residual eggs. Testes may contain remains of sperm.

The biological data dealt with are from annual reports published by ØSTVEDT (1961, 1962, 1965, 1966), DEVOLD and ØSTVEDT (1963, 1964) and DRAGESUND (1967, 1968a, 1968b) and from unpublished records available at the Institute of Marine Research, Bergen. Statistical information on the Norwegian landings was obtained from annual reports on the Norwegian herring fisheries (ANON. 1960–1966a). The method used to estimate the adult stock size has been described by DRAGESUND and JAKOBSSON (1963), where estimates for the period 1952–1959 are also given. For the years 1964 and 1965 unpublished data are available at the Institute of Marine Research, Bergen, and the Fisheries Research Institute, Reykjavik.

LARVAL HERRING

The larvae were collected on surveys covering the Norwegian coastal banks from Stad to Lofoten (WIBORG 1960, 1961, 1962a, 1962b, DRAGESUND and WIBORG 1963, DRAGESUND 1965, DRAGESUND and HOGNESTAD 1966). The area was usually surveyed twice and the sampling was carried out from south to north and south again with one research vessel. Oblique hauls were taken with Clarke–Bumpus plankton samplers (CBPS) with a tube aperture of 13 cm diameter (CLARKE and BUMPUS 1950). The length of the nylon or silk nets used was 60 cm with a mesh size of 0.50 mm. The CBPS were equipped with flowmeters and two samplers were towed simultaneously at different depths and raised in 5 m steps. The sampling depths were 25–5 m, 50–30 m, and occasionally 75–55 m. The total towing time was 20 minutes. A weight of 28 kg was attached at the end of the 4 mm thick wire, which was kept as close as possible to an angle of 50° from the surface by keeping the towing speed between 1.5 and 2.0 knots.

Because of difficulties in operating the closing mechanism of the CBPS in bad weather, this was permanently kept in an open position. The bias caused by this is considered to be of little importance, except when larval density in the uppermost depth interval is high compared with the depth intervals below.

In 1959 sampling with CBPS was carried out during a relatively late period (20–28 April) in the second part of the survey only. However, larvae were collected during the entire 1959 survey in vertical hauls from the bottom to the surface with a 1 m diameter Nansen net (NANSEN 1915). Sampling with Isaacs–Kidd three-foot midwater trawl (IKMT) (ARON 1962) was made at selected stations during the 1964 survey.

The larvae were preserved in diluted formalin containing 4% formaldehyde. At the laboratory they were counted and measured to the nearest mm below and classified as larvae with or without yolk sac. According to BLAXTER (1968) herring larvae shrink about 12% in length in a fixative of the type used. The shrinkage of the larvae was not taken into account when working out the length distributions, but since the larvae were preserved and measured in the same way each year the length distributions are assumed to be comparable from year to year.

To facilitate comparison between stations and from year to year, the number of larvae collected with CBPS was converted to numbers below 1 m^2 of surface by multiplying the original numbers for each station with the sampling interval and then dividing by the water volume filtered. For analysis of vertical distribution the number of larvae per 1 m^3 water was calculated. The number of larvae collected with the Nansen net was converted to numbers below 1 m^2 of surface by dividing the number of larvae caught by the area (in m^2) of the net aperture. The abundance estimates obtained by CBPS and Nansen net are not comparable.

LARVAL DRIFT

Freely floating drogues were used at several localities in 1964 and 1965 in order to study the drifting velocity of larvae. The drogue was made of two iron sheets having the dimensions of $0.2 \times 100 \times 100$ cm and fixed at right angles to each other. The drogue was suspended by a 1.6 mm thick nylon line from a plastic float to which a pole was attached. The pole was equipped with a light on the top, about 2 m above the surface. The positions of the drogues were determined by Loran and radar. In addition the larval drift pattern was deduced from wind observations and drift bottle experiments.

The wind data are from the meteorological stations Ona (N 62° 54′, E 06° 30.5′), Nordøyane (N 64° 48′, E 10° 33′) and Skomvær (N 67° 25′, E 11° 53′) as reported in Norsk Meteorologisk Årbok (ANON. 1960–1966b). Wind forces are given in Beaufort units and wind directions in twelve sectors, each covering 30°. The wind observations were transformed into monthly wind vectors. These were obtained by multiplying for each direction and month the mean wind force with the frequencies of observations of wind in the particular direction and thereafter the resultant vector was constructed from those established for each direction.

In 1961, 1963, 1964 and 1965 drift bottles were released in larval patches at various places along the coast. The bottles had an inner volume of 350 ml and weighed 530 g. A letter inside each bottle requested the finder to report the date and place of recovery.

EVALUATION OF FACTORS AFFECTING LARVAL ABUNDANCE ESTIMATES

Several methods have been employed to estimate the annual abundance of planktonic fish eggs and larvae (e.g. BUCHANAN-WOLLASTON 1926, SETTE and AHLSTROM 1948, TAFT 1960, SAVILLE 1963). ENGLISH (1963) analysed some common procedures of estimating annual abundance of planktonic fish eggs. The data used were treated by analysis of variance and he concluded that the major source of variability in estimates of annual egg abundance is the time effect. This is mainly due to the unknown fluctuations in time and location of maximum egg abundance. The number of stations was less important and duplications (paired hauls) were least important.

Reliable estimates of annual abundance of larvae are more difficult to obtain than for planktonic eggs, especially because of net avoidance and variation in diurnal behaviour of the larvae. In the present work, therefore, no attempt will be made to estimate the total abundance of herring larvae at hatching or at subsequent stages. The low number of surveys (usually two per season) and the long distance between stations (about ten nautical miles) do not allow for such estimates. Moreover, the sampling time was not always the same relative to the time of spawning. The numerical values obtained, therefore, are used only to show trends in the geographical distribution and to give some estimates of larval abundance at selected sections. The distribution charts were made by plotting the figures for each station and drawing isolines of abundance.

The haul-to-haul variation in oblique hauls with CBPS was investigated at some stations during the 1964 survey by comparing the number of larvae caught:

1) at the same station in two subsequent hauls (Table I);
2) in two samplers attached above each other, 1 m apart (Table II).

An analysis of variance was applied to these data using a log-transformation, log $(x+k)$, where x is the number of larvae below 1 m^2 of surface and $k=1$ (CASSIE 1968). The calculations (Tables 1 and 2) show that

Table 1. Analysis of variance of the data in Table I.

Source of variation	Sums of squares	Degrees of freedom	Variance of estimate	Value of F	Probability
Between series of haul	0.036	1	0.036		
Between hauls	7.675	15	0.512		
"Residual"	0.806	15	0.054	0.667	>0.05
Total	8.517	31			

Table 2. Analysis of variance of the data in Table II.

Source of variation	Sums of squares	Degrees of freedom	Variance of estimate	Value of F	Probability
Between series of haul	0.004	1	0.004		
Between hauls	17.471	20	0.874		
"Residual"	0.628	20	0.031	0.129	>0.05
Total	18.103	41			

there was no significant difference ($P > 0.05$) in numbers between series of hauls or between catches from approximately the same depth. The results from this analysis indicated that the larvae were evenly distributed within the relatively small area sampled. The error caused by the variability in catch of replicate hauls in the same body of water is therefore assumed to be relatively small compared with that introduced by taking a sample over a small area as being representative of a much larger area.

Knowledge of the avoidance of sampling devices by planktonic organisms (including fish larvae) has been reviewed by CLUTTER and ANRAKU (1968). Even if the results are contradictory the accumulated data indicate that avoidance occurs. They reported that the catching efficiency increases with increasing speed of the net, and that larger fish larvae avoid nets towed at low speed to a greater extent than do the smaller larvae. It is assumed, therefore, that CBPS being towed at 1.5–2.0 knots will catch the fish larvae less efficiently than will high speed samplers, e.g. the Gulf III (GEHRINGER 1952).

In order to evaluate the effect of avoidance by herring larvae for CBPS, comparisons were made of the length distributions of larvae caught with IKMT and CBPS. Moreover, comparisons were made of the length distributions in catches taken by CBPS around subsurface drogues at night and during the day. The IKMT generally caught larger larvae than the CBPS (Table 3). However, no significant difference in mean length was found for the smallest larvae. Larger larvae were caught at night at drift stations 2 and 5 (off Sklinna and Frøya), whereas at drift station 4 (off Eggum) they occurred in the samples during the daytime (Table 4).

The diurnal variation in catches was analysed by sampling larvae at different depth layers around subsurface drogues every second hour during a 24-hour period at the three mentioned drift stations (Table III). At station 2 (off Sklinna) the number of larvae caught at night was significantly higher than at daytime ($P < 0.05$), whereas at stations 4 and 5 (off Eggum and Frøya) no significant difference was found (Table 5).

Although the results are somewhat ambiguous it is assumed that the net avoidance will affect both length distributions and abundance esti-

Table 3. Comparison between mean lengths ($\bar{l}$) of larvae caught with IKMT and CBPS during the 1964 survey.

Locality	Date	Hour	Gear	Depth in m	No. of larvae	$\bar{l}$ in mm	Standard deviation	Value of Student's t	Probability
Off Halten	16.4	1724–1910	IKMT	25–5	7	12.7	1.20	0.362	>0.05
			CBPS	25–5	7	12.4	1.84		
Off Sklinna	18–19.4	1920–1540	IKMT	50–30	113	14.9	1.97	0.746	>0.05
			CBPS	50–30	16	15.3	2.26		
Off Eggum	28–29.4	1455–0910	IKMT	50–30	84	12.2	2.26	0.152	>0.05
			CBPS	50–30	334	12.1	1.53		
Off Træna	1.5	0145	IKMT	50–30	159	18.2	1.95	8.257	<0.05
		0105	CBPS	50–30	27	14.7	3.74		
		0558–0820	IKMT	50–30	90	17.2	2.43	4.380	<0.05
		0524–0741	CBPS	50–30	16	14.2	3.03		
Off Sklinna	2.5	0227	IKMT	50–30	42	18.7	2.18	4.632	<0.05
		0150	CBPS	50–30	30	14.9	4.66		
Off Halten	3.5	0228	IKMT	50–30	63	21.1	1.65	3,717	<0.05
		0150	CBPS	50–30	5	18.0	3.32		
		1047	IKMT	50–30	23	16.3	2.21	0.455	>0.05
		1055	CBPS	50–30	3	15.7	1.25		
Off Grip	4.5	0543	IKMT	50–30	1	19.0	—		
		0343	CBPS	50–30	4	14.3	2.94		

Table 4. Comparison between mean lengths ($\bar{l}$) of larvae caught by night and by day in oblique hauls from 50 to 5 m with CBPS at three drift stations.

Drift station no.	Date		Time	No. of larvae	$\bar{l}$ in mm	Standard deviation	Value of Student's t	Probability
2	1964	18–19.4	Night	244	16.1	1.95	1.983	<0.05
			Day	94	15.6	2.37		
4	1964	28–29.4	Night	505	12.0	1.54	2.494	<0.05
			Day	1275	12.2	1.52		
5	1965	9–10.4	Night	157	12.2	1.49	5.359	<0.05
			Day	271	11.5	1.18		

Table 5. Analysis of variance of the data in Table III. The calculations were made on the log (x+1) transformation.

Drift station no.	Source of variation	Sums of squares	Degrees of freedom	Variance of estimate	Value of F	Probability
2	Between day and night	1.468	1	1.468		
	Within day and night	1.570	11	0.143	10.290	<0.05
	Total	3.038	12			
4	Between day and night	0.015	1	0.015		
	Within day and night	0.192	11	0.017	0.882	>0.05
	Total	0.207	12			
5	Between day and night	0.284	1	0.284		
	Within day and night	0.851	10	0.085	3.341	>0.05
	Total	1.135	11			

mates, especially when the larvae are longer than 15 mm. However, since there was no clear diurnal variation in the catches, it was not considered necessary to apply any conversion factor to make catches comparable to those taken by night.

During the 1959 and 1960 surveys sampling with CBPS was carried out only from 25 to 5 m, and to make the catches comparable with the following years a conversion factor was estimated and used to compensate for the lack of sampling in 50–30 m. The number of larvae caught at each station during the 1959 and 1960 surveys at depths of 25–5 m was multiplied by a factor of 1.7, which is the ratio between the number of larvae caught at 50–5 m and 25–5 m, respectively, during the cruises in 1961–1965. Larvae also occur below 50 m and the larval abundance is, therefore, underestimated by the present sampling procedure. However, samples are scarce from depths below 50 m, and no attempt has been made to compensate for this underestimate.

SPAWNING CHARACTERISTICS

SPAWNING STOCK

During the period 1959–1962 the spawning stock had only one component which migrated towards the coast off Møre (area 07) from the usual wintering area east of Iceland (Devold 1963). The major part of the stock again approached the coast from this wintering area in 1963–1965, but a second component migrated towards the Lofoten region (area 05) from another wintering area, located off the coast between Torsvåg and North Cape (Devold 1968). The herring arrived off Møre at the end of January and during February. The other component reached the Lofoten spawning grounds three to four weeks later, except in 1965.

In 1959–1963 the rich 1950 year-class dominated in the spawning stock off Møre (Table 6). In 1963 the age structure of the stock changed as recruit spawners from the 1959 year-class appeared in the catches. In 1964 and 1965 this year-class dominated in the spawning stock both off Møre (area 07) and at Lofoten (area 05), but herring of the 1960 and the 1961 year-classes were also present on the spawning grounds. In 1965 these three year-classes made up 80–85% of the total catches off Møre. The spawning stock at Lofoten consisted almost entirely of the 1959–1961 year-classes.

In 1959 recruit spawners constituted 11.7% of the herring caught off Møre and 21.3% of those caught between Bokn and Stolmen (Table 7). During the seasons in 1960–1963 the percentage of recruit spawners was considerably lower, except in 1963 at Lofoten where only recruit spawners were recorded. In 1964 and 1965 recruit spawners made up 34.4% and 35.9% respectively of the herring off Møre with the corresponding percentages for the Lofoten region being 93.7% and 76.4%.

Estimates of the absolute size of the spawning stock based on tagging experiments are available for the years 1952–1959 and 1964–1965 (Dragesund and Jakobsson 1963, Anon. 1969). Estimates obtained from combined acoustic surveys and underwater photography experiments for the years 1959 and 1962–1965 are also available (Fedorov, Truskanov and Yudanov 1963, Anon. 1969). The results are illustrated in Fig. 2. The average figures are given for years when both methods have been used.

Table 6. Age composition (in %) of Norwegian herring caught with purse seine during the spawning seasons in 1959–1968.

Year	Area	Total no.	Year-class															Mean age
			1963	1962	1961	1960	1959	1958	1957	1956	1955	1954	1953	1952	1951	1950	<1950	
1959	08	553						—	—	0.4	1.3	4.0	17.4	6.0	8.0	51.8	11.1	8.4
	07	2106						—	—	—	0.7	1.1	7.1	5.7	8.4	54.1	22.9	9.5
	06	94						—	—	—	—	—	2.1	3.2	4.2	73.4	17.1	9.5
1960	07	3038					—	—	—	0.2	1.4	1.2	6.1	3.6	5.3	64.4	17.8	10.3
1961	07	666				—	—	—	0.4	0.9	3.3	2.9	7.7	4.8	6.5	59.0	14.5	10.7
1962	07	992			—	—	0.1	—	0.5	1.0	2.7	1.5	7.8	4.2	6.6	62.7	12.9	11.7
	06	80			—	—	—	—	—	—	—	1.3	11.2	2.5	7.5	73.7	3.8	11.7
1963	07	923		—	—	—	4.0	0.3	0.4	0.7	1.8	1.7	8.7	3.6	8.3	61.1	9.4	12.2
	06	314		—	—	—	13.1	0.3	—	—	—	0.3	7.3	3.2	7.3	62.5	6.0	11.6
	05	433		—	—	9.5	89.8	0.7	—	—	—	—	—	—	—	—	—	3.9
1964	07	1198	—	—	—	4.0	51.5	0.4	0.2	0.7	1.3	0.5	4.2	2.2	3.2	28.0	3.8	8.7
	05	1089	—	—	0.6	10.1	88.4	0.3	—	—	—	—	0.1	—	—	0.5	—	4.9
1965	07	1141	—	—	3.2	10.7	62.7	0.1	0.2	—	0.4	0.9	2.0	1.4	2.2	14.4	1.8	7.8
	06	96	—	—	18.8	26.0	55.2	—	—	—	—	—	—	—	—	—	—	5.4
	05	719	—	—	5.8	19.6	74.1	0.1	—	—	—	—	0.3	—	—	—	0.1	5.7
1966	07	2963	—	0.1	10.3	27.7	53.4	0.2	0.2	0.1	0.2	0.3	0.7	0.7	0.4	5.2	0.5	7.2
	06	471	—	—	3.6	25.1	60.8	—	—	0.2	—	—	0.6	0.6	0.2	8.5	0.4	7.6
	05	749	—	0.3	8.0	39.1	51.6	0.3	—	—	—	—	—	0.1	0.3	0.3	—	6.5
1967	07	2135	0.5	0.4	13.4	32.1	48.8	0.1	0.1	0.1	0.2	0.3	0.7	0.3	0.3	2.6	0.1	7.3
	06	99	1.0	—	10.1	41.4	46.5	1.0	—	—	—	—	—	—	—	—	—	7.4
1968	07	1352	0.7	1.7	13.8	34.2	46.9	0.2	—	0.1	0.2	0.2	0.7	0.3	—	1.0	—	8.5
	06	243	0.8	1.2	9.9	34.6	51.5	—	—	—	—	—	0.4	—	—	1.2	0.4	8.6

Table 7. Composition (in %) of recruit and repeat spawners of Norwegian herring during the spawning seasons in 1959–1965.

Year	Area	Region	No.	Recruit spawners	Repeat spawners
1959	08	Bokn-Stolmen	816	21.3	78.7
1959	07	Stad-Frøya	1761	11.7	88.3
1960	07	Stad-Frøya	3991	3.9	96.1
1961	07	Stad-Frøya	2610	1.0	99.0
1962	07	Stad-Frøya	2842	0.5	99.5
1963	07	Stad-Frøya	1938	5.2	94.8
1963	05	Off Lofoten	434	100.0	—
1964	07	Ona-Frøya	2097	34.4	65.6
1964	05	Off Lofoten	1176	93.7	6.3
1965	07	Ona-Grip	1270	35.9	64.1
1965	06	Off Halten	96	87.5	12.5
1965	05	Off Lofoten	643	76.4	23.6

The stock estimates for the 1952–1965 period vary between 2.5 and 20.0 million tons with the highest figures for 1952–1956. From 1957 onwards a rapid decrease in the stock took place and this continued until 1962 when it was about 2.5 million tons. In the following three years the stock increased from 2.9 million tons in 1963 to 7.3 million tons in 1965

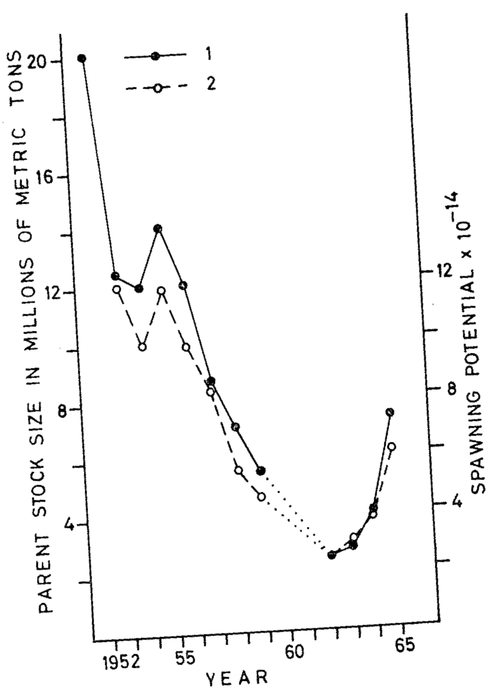

Fig. 2. Variation in, (1) parent stock size of Norwegian herring during the spawning seasons in 1952–1965 and (2) number of eggs spawned (spawning potential).

due to recruitment from the rich 1959 year-class. The estimates for 1963–1965 do not include the component spawning off Lofoten, and the total spawning stock in these years, therefore, is underestimated. Abundance indices obtained from data on catch per unit effort (ØSTVEDT 1963) indicated that the estimate of the stock size for 1952 is too high. The figures for the period 1953–1959 follow the same trend as the abundance indices given by ØSTVEDT.

The spawning potential of the stock is positively correlated to the size of the stock. However, fecundity (the number of eggs in the gonads of individual fish) increases with length and weight of the fish, and thus the spawning potential of the stock is a function both of the number and the length distribution of fish. In order to analyse the year by year variations of the spawning potential, the stock size in tons in the different years were converted to numbers of fish by length. Length and weight data of herring collected from purse seine catches were used to give stock estimates in tons for the different length groups. The estimated stock sizes in weight by length were then divided by the corresponding mean weight of herring in each length group. The sex ratio of spawning Norwegian herring is approximately 1:1 (DRAGESUND unpublished). With data on fecundity by length (PARRISH and SAVILLE 1965), the number of eggs deposited each year, therefore, could be calculated (Fig. 2). The variations in the spawning potential follow the same trend as that of the stock estimates in tons. However, in years when young individuals dominated in the spawning stock, as in 1954–1956 (ØSTVEDT 1963) and in 1964–1965, the spawning potential was relatively low compared to years when the stock consisted of old individuals, as in 1962–1963.

The following characteristic features concerning the structure and size of the spawning stock during the period 1959–1965 can be listed:

1) the mean age of the stock increased from 1959 to 1963 with the 1950 year-class predominating;
2) the 1959 year-class dominated in the stock in 1964 and 1965 and the percentage of recruit spawners was highest these years;
3) the stock size had its lowest values in 1961–1963 and its highest in 1965;
4) the stock size was on a considerably lower level in 1959–1965 than in the mid 1950s.

LOCATION AND TIME OF SPAWNING

The spawning grounds were located by studying the geographical distribution of catches of spawning and spent herring and by surveying the coastal banks for newly hatched larvae. Herring remain on the same grounds from just before spawning until they gradually migrate from the coastal banks. The distribution of catches during the spawning season, therefore, will give information on the location of spawning (Fig. 3). The occurrence of larvae with yolk sac indicates that spawning must have taken place not very far from the locality of capture. The distribution of yolk sac larvae coincided fairly well with the distribution of catches of spawning and spent herring (Fig. 3). However, in some years the larvae were found distributed slightly to the west and north of the herring catches. This could be expected since the yolk sac stage lasts for some days, about ten days at 8°C (Blaxter and Hempel 1963), and a dispersion from the spawning grounds evidently takes place during this time. In 1964 the survey was made late in relation to the main spawning season, and therefore only few yolk sac larvae were found in areas 07 and 06 that year.

Although the data are insufficient for a precise determination of the spawning grounds, it can be concluded that spawning was concentrated within four following areas:

1) area 08, between Bokn and Stolmen;
2) area 07, between Kinn and Frøya;
3) area 06, between Halten and Sklinna;
4) area 05, off the Lofoten Islands.

During the period 1959–1965 the most important spawning took place in area 07. In 1959–1962 the majority of the herring in this area tended to concentrate somewhat farther south (between Stad and Ona) than in 1963–1965, when the centre of spawning was located between Ona and Grip. Spawning in area 08 was negligible except in 1959 when spawning was observed at certain places along the coast as far south as Bokn. The spawning between Halten and Sklinna (area 06) occurred regularly and did not show any change in location. Mass spawning off the Lofoten Islands (area 05) was not recorded during the period 1959–1962. However, a few yolk sac larvae caught in this region in 1960 suggest spawning there that year. From 1963 to 1965 herring spawned regularly at Lofoten.

The distribution of relative catches of spawning and spent herring presumably give the best indication of the geographical distribution of the spawning area. In Table 8 the number of rectangles shown in Fig. 3 in which spawning and spent herring were caught, is listed. For 1960 and 1961, within area 06, the distribution of yolk sac larvae was used. The spawning was restricted to grounds with sandy or rocky bottom, and not all the grounds within the rectangles shown in Fig. 3 constitute localities for spawning. Within the two southern spawning areas (08 and 07) a restriction in the geographical distribution of the catches were found from

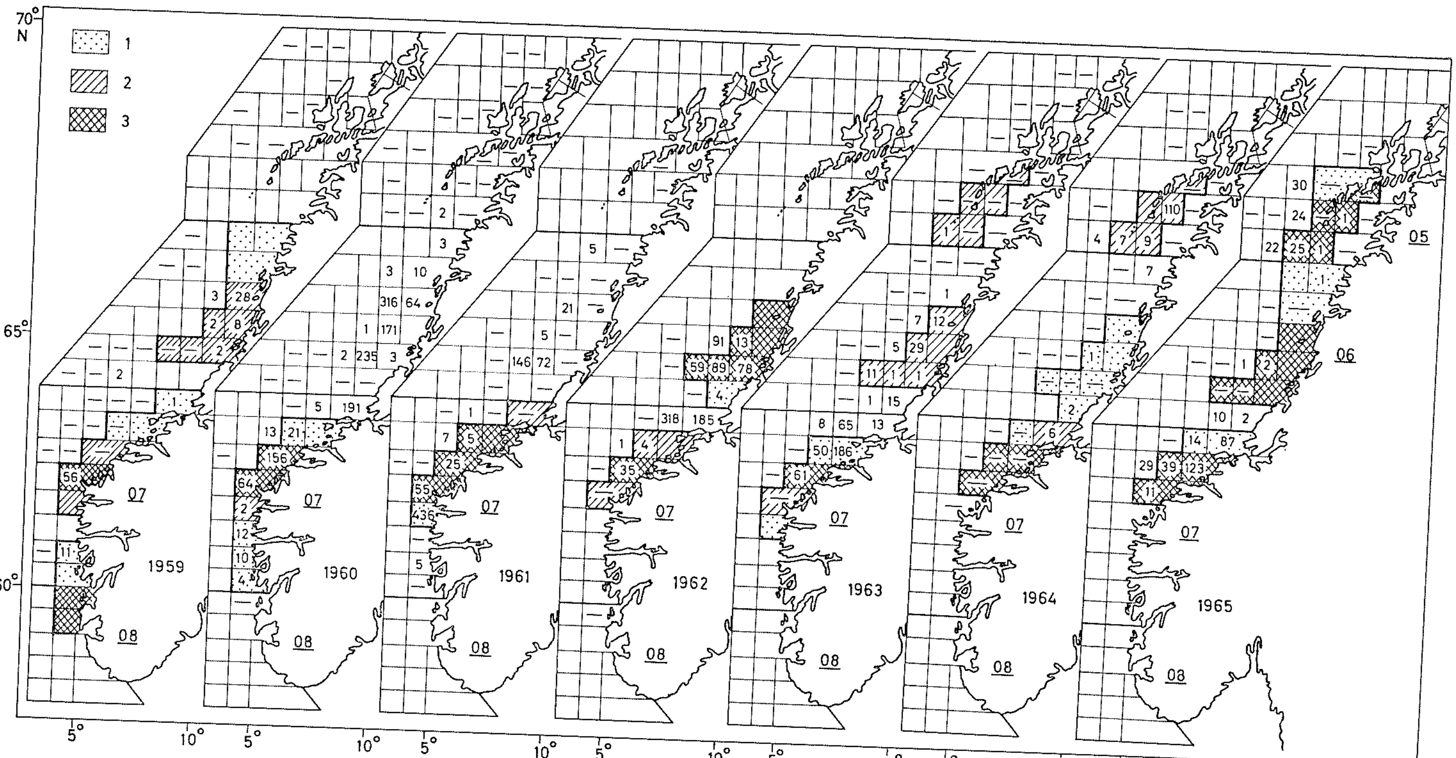

Fig. 3. Distribution of relative catches of spawning and spent herring during the Norwegian winter herring seasons in 1959–1965. Legend: (1) <5%, (2) 5–15% and (3) >15% of the total catches, respectively. The figures in the rectangles denote numbers of yolk sac larvae per station below 1 m² of surface. The horizontal lines denote hauls without larvae.

1959 to 1965, accompanied with an increase in the extension within area 05 from 1963 to 1965. The extension of the spawning area seemed to decrease with the size of the spawning stock, being most restricted in 1961 and 1962.

Table 8. Extension of spawning area indicated by number of rectangles shown in Fig. 3 in which spawning and spent herring were caught in 1959–1965.

Area	Spawning year						
	1959	1960	1961	1962	1963	1964	1965
08	2	0	0	0	0	0	0
07	8	8	6	4	5	5	5
06	9	9?	5?	7	6	7	9
05	?	?	?	?	5	5	6

Even in the same locality groups of herring which keep together will spawn at slightly different times. The time of the main spawning is estimated from the composition of the various maturity stages of herring in samples collected just prior to and during the spawning season. The duration of the spawning season is defined as the time between the first and last occurrence of herring in stage VII.

In Fig. 4 the relative frequency for the different maturity stages is plotted against time (in five-day periods). The data used in the figure are listed in Table IV. The time when the first fish were found in maturity stage VII, indicating the commencement of spawning (T_1), could be determined fairly accurately, but the time for the end of spawning (T_2) was more difficult to assess from the present material since some herring in stage V occurred in samples collected even at the end of the sampling period. These herring had to pass through stage VI before the season could be considered ended. The duration of stage VI for the individual fish is incompletely known for Norwegian herring, but this stage is the shortest (ILES 1964). To get approximate figures for the duration of stage VI, the time interval between the first occurrence of stages VII and VI (T_d) was measured. By adding T_d to the last time when herring in maturity stage V occurred, the end of the spawning season (T_2) was estimated. The time of the main spawning is defined to occur at the mid-point between T_1 and T_2 (Fig. 4).

In area 07 (off Møre) spawning commenced relatively early in 1959, 1960 and 1965, when the main spawning took place in the first week of March. In 1962 and 1963 the onset of spawning was late and the main spawning occurred 15–19 and 10–14 March, respectively. The duration of the spawning seasons in 1959–1965 was longest in 1959, 1960 and 1961,

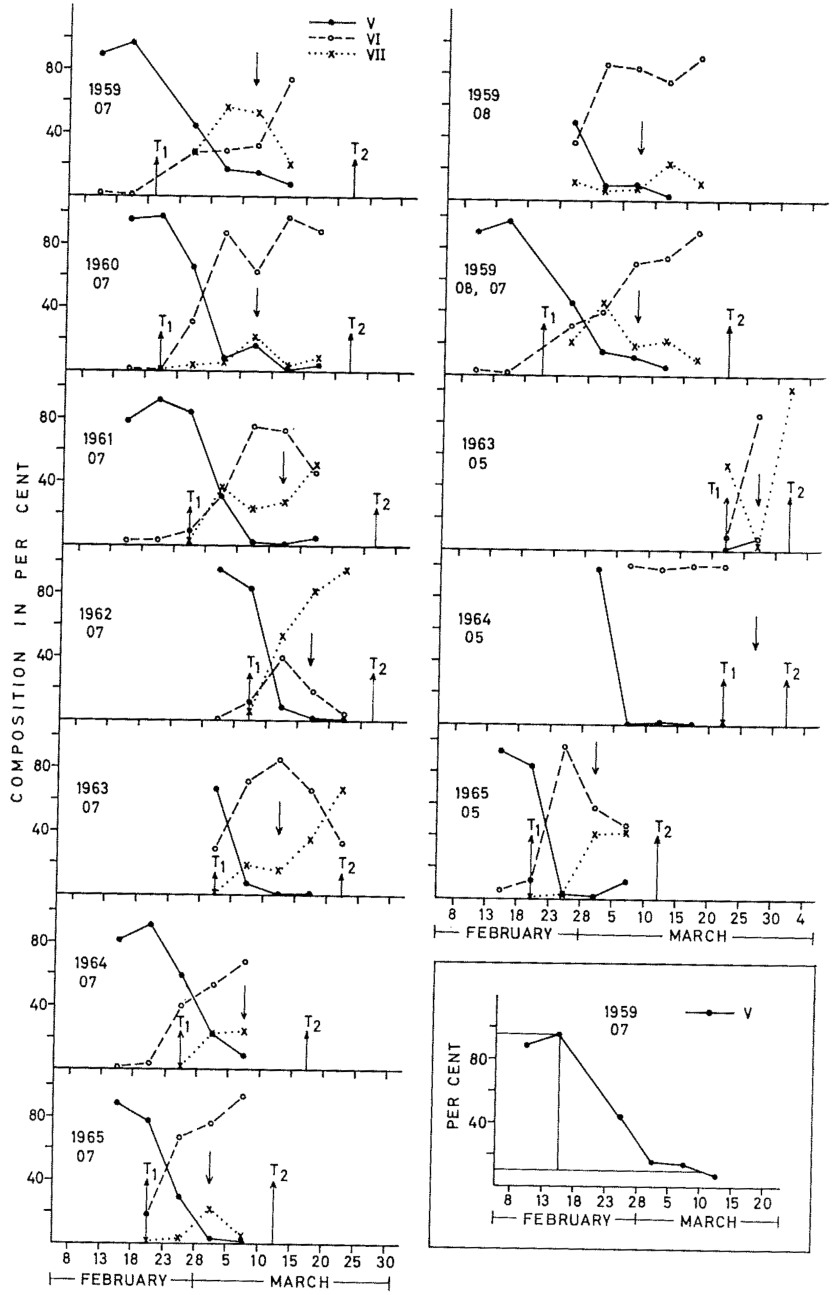

Fig. 4. Maturity composition (in %) of stages V–VII in samples of Norwegian herring collected during the spawning seasons in 1959–1965. Data for males and females are pooled and plotted against time in five-day periods. T_1 and T_2 represent the onset and end of spawning. The time of main spawning is indicated as the midpoint between T_1 and T_2 by an unlabelled arrow. The inserted illustration of the method used to estimate the spawning rate by measuring the reduction of stage V is explained in the text.

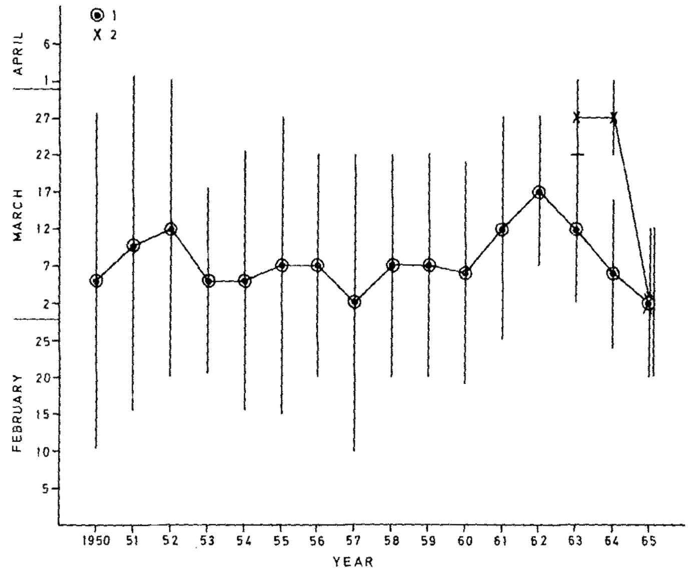

Fig. 5. Time of main spawning during the period 1950–1965, (1) within areas 07 and 08 and (2) within area 05. Vertical bars denote duration of the spawning season.

lasting for about one month. In the other years the season lasted only about three weeks.

In area 06 (between Halten and Sklinna) the duration of spawning in 1959 could not be studied in the same detail because of the limited number of samples available. Apparently, spawning occurred almost at the same time or slightly later than in area 07. Herring examined from the Halten Bank showed that spawning commenced a few days later there than elsewhere in area 06. In area 05 (off Lofoten) the onset of spawning was late in 1963 as well as in 1964, and lasted only about ten days. In 1965 the onset and duration of spawning were the same as in area 07.

In Fig. 5 the time of the main spawning and the duration of the spawning season are illustrated for the period 1959–1965, supplemented with data from the spawning seasons in 1950–1958. No special trend in time of the main spawning was found during the period 1950–1965. However, the spawning seasons lasted somewhat longer in 1950–1958 than during the period 1959–1965, probably because of the restricted spawning in the southernmost region within area 08.

In the spawning seasons of 1964 and 1965 the influx of recruits was high. A comparison between the onset of spawning for recruit and repeat spawners these years is given in Table 9. Apparently no marked difference

Table 9. Composition (in %) of the maturity stages of Norwegian herring in five-day periods during the spawning season in 1964 and 1965.

Area	Date		Recruit spawners					Repeat spawners				
			No.	Maturity stage				No.	Maturity stage			
				IV	V	VI	VII		IV	V	VI	VII
07	1964	13–17.2	137	20.4	78.8	0.8	—	228	17.1	82.9	—	—
		18–22.2	223	9.0	87.0	4.0	—	238	0.8	95.4	3.8	—
		23–27.2	208	1.4	57.7	39.4	1.5	428	0.2	59.6	39.7	0.5
		28.2–3.3	83	1.2	26.5	54.2	18.1	237	0.4	21.2	52.7	25.7
		4–8.3	71	—	14.1	71.8	14.1	224	—	7.4	65.6	27.0
05	1964	28.2–3.3	79	2.5	97.5	—	—	3	—	100.0	—	—
		4–8.3	80	—	—	100.0	—	14	—	—	100.0	—
		9–13.3	92	—	2.2	97.8	—	3	—	—	100.0	—
		14–18.3	513	—	0.2	99.8	—	27	—	—	100.0	—
		19–23.3	338	—	—	99.1	0.9	27	—	—	100.0	—
07	1965	13–17.2	115	26.1	73.9	—	—	202	3.0	97.0	—	—
		18–22.2	146	9.6	72.6	17.8	—	258	—	79.8	19.8	0.4
		23–27.2	45	2.2	33.3	57.8	6.7	203	—	29.0	68.0	3.0
		28.2–4.3	110	1.8	1.8	63.6	32.8	95	—	5.3	88.4	6.3
		5–9.3	40	—	2.5	95.0	2.5	56	—	—	92.9	7.1
06	1965	15–19.3	84	—	—	92.9	7.1	12	—	—	100.0	—
05	1965	13–17.2	70	2.9	91.4	5.7	—	25	—	96.0	4.0	—
		18–22.2	129	5.4	86.0	7.8	0.8	46	2.2	76.1	21.7	—
		23–27.2	71	—	2.8	94.4	2.8	23	—	—	100.0	—
		28.2–4.3	142	—	2.2	57.0	40.8	45	—	—	60.0	40.0
		5–9.3	79	1.3	12.7	49.6	36.4	13	—	—	30.8	69.2

was found in the onset of spawning although repeat spawners reached maturity stages VI and VII a little earlier than the recruits. This suggests that recruits spawned slightly later than the repeat spawners, especially in area 07.

The transition from the prespawning to the spawning stage was studied by estimating the rate of reduction for the maturity stage V from the maximum frequency points of the stage V curves to their 10% levels. The percentage reduction was measured (Fig. 4) and the reduction per day (defined as the spawning rate) was estimated (Table 10). The figure for 1962 (area 07) indicates mass spawning over a relatively short period, whereas in 1959 spawning took place at a considerably slower rate. The spawning in the other years occurred at a more moderate rate than in 1962. In area 05 (off Lofoten) the spawning rate was generally higher than in area 07 (off Møre), especially in 1964.

Table 10. Spawning rate of Norwegian herring indicated by the percentage reduction of the maturity stage V per day (see text for explanation).

Area	Spawning year						
	1959	1960	1961	1962	1963	1964	1965
07	3.8	5.9	6.3	8.7	—	5.3	5.3
05	—	—	—	—	—	22.0	10.3

TIME OF HATCHING

The time of main hatching can be found by adding the incubation period to the time of main spawning. Knowing the temperature on the spawning grounds, an approximate figure for the incubation period can be estimated (BLAXTER and HEMPEL 1963). The incubation period varies from about twenty-five days at 5 °C to about sixteen days at 8 °C. Investigations carried out off Møre (unpublished) during the spawning seasons in 1967 and 1968, showed that the spawning took place at depths less than 250 m, with the most frequent spawning depths ranging from 50 to 200 m. Therefore, the mean temperature between 50 and 200 m (or bottom) in the different regions was used in order to estimate the incubation period (Fig. 6). The stations were located on the main spawning grounds within each region. The number of stations varied between two and four. The mean temperature in the spawning region off Møre (area 07) was lowest in 1959 and 1963 resulting in a correspondingly longer incubation period than in the other years. The quartile intervals, indicat-

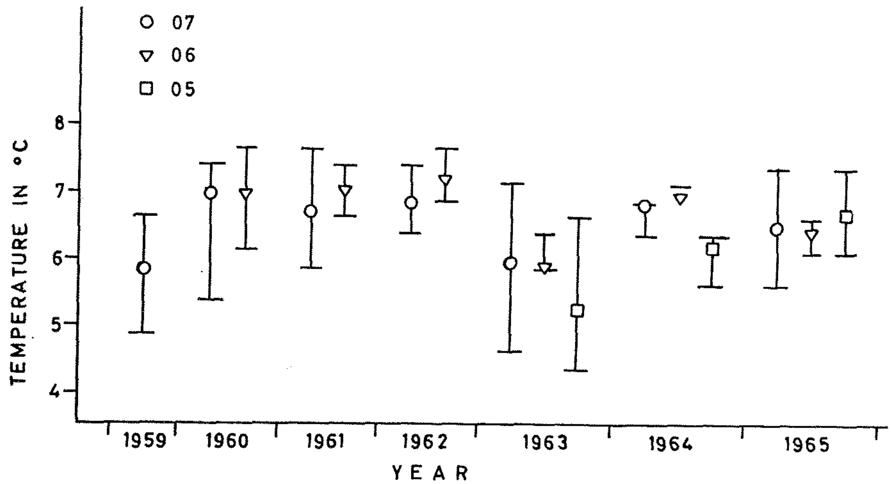

Fig. 6. Mean temperature at different spawning grounds within the main spawning regions in areas 07, 06 and 05, depth intervals from 50 to 200 m or to the bottom. The vertical bars show the quartile intervals.

ing the temperature range within the main spawning depths, were widest in 1959, 1960, 1963 and 1965 and this feature may have resulted in a variable incubation period (Fig. 7). The range was considerably more narrow in 1962 and 1964 and the time of main hatching, therefore, shorter. In the spawning regions off Halten–Sklinna and Lofoten (areas 06 and 05) the mean temperature followed the same trend as in area 07, but the quartile intervals in area 06 was not as wide as on the spawning grounds within area 07. Since the spawning occurred at different times off Møre (area 07) and Lofoten (area 05) in 1963 and 1964, the total hatching period was relatively long these years. In 1965 the spawning and hatching took place almost at the same time in the two spawning regions and the time of main hatching occurred relatively early, especially in area 05 (Fig. 7).

The commencement of the Norwegian winter herring fishery, coinciding in time with the arrival of spawners to the coast, the estimated time of the main spawning and hatching and the first and second periods of larval sampling are also plotted on the time scale in Fig. 7. On the Møre coast (area 07) the time of arrival of the herring, the spawning and the subsequent hatching all occurred progressively later during the period 1959–1962, whereas the opposite trend was found from 1963 to 1965.

Fig. 7. Time of, (1) commencement of the Norwegian winter herring fishery, (2) main spawning, (3) main hatching, (4) and (5) first and second annual periods of larval sampling.

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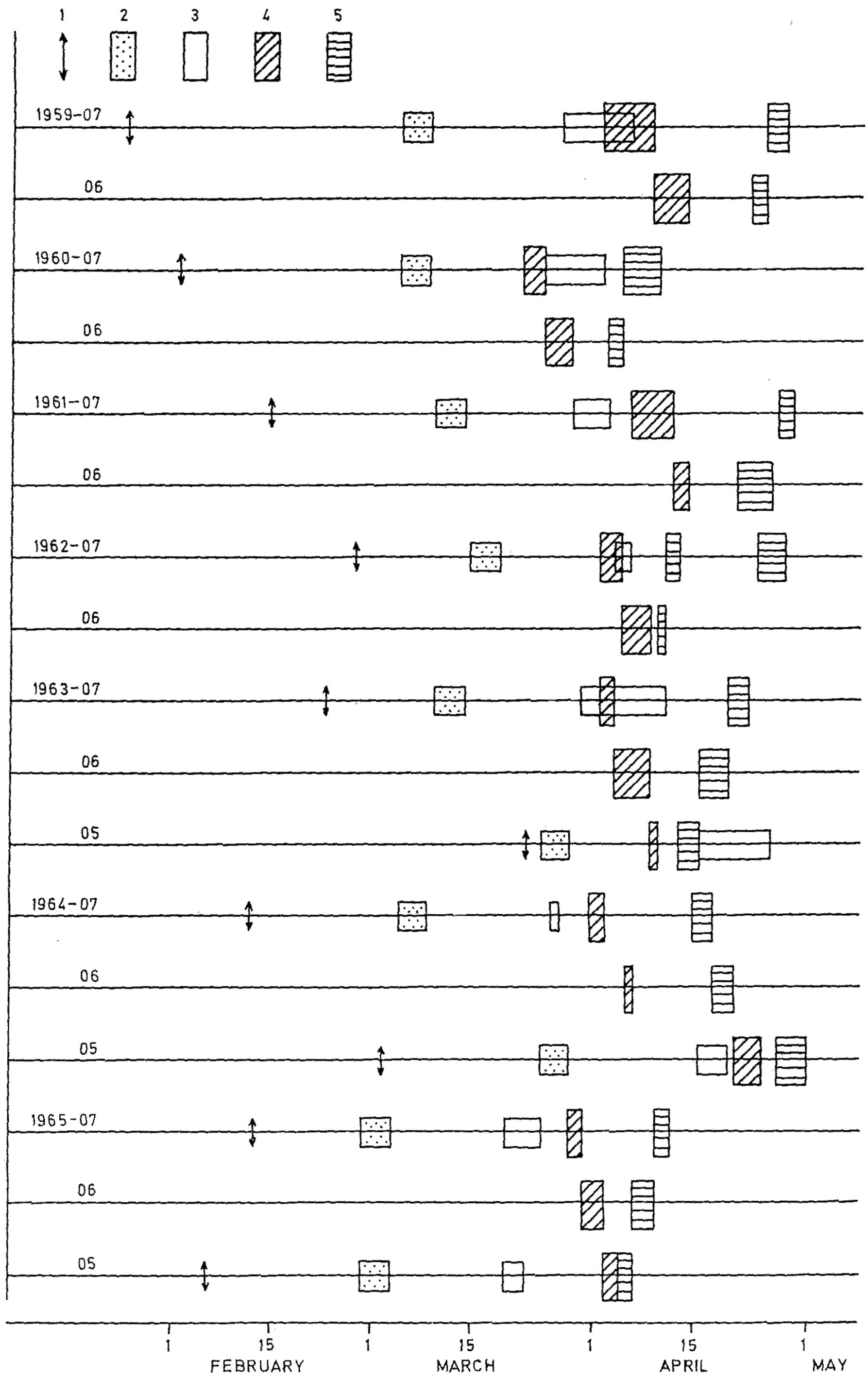
1
2
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THE LARVAE

LARVAL DISTRIBUTION AND ABUNDANCE IN RELATION TO SPAWNING CHARACTERISTICS AND WATER CURRENTS

Soon after hatching the major part of the larvae rise into the upper water layers (50–0 m). Observations made at drift stations off Sklinna and Eggum indicated a vertical migration of the larvae (Fig. 8). During the dark, larvae were most abundant in the upper 20 m and by day they concentrated at a depth between 20 and 40 m. However, a higher net avoidance during the day might to some extent account for the variation in vertical distribution within the upper 40 m. Nevertheless the majority of the larvae did occur within the upper 50 m and were scarce in the depth range from 50 to 70 m.

The larvae are transported northwards mainly in coastal water, i.e. water with salinity less than 35‰ (HELLAND-HANSEN and NANSEN 1909). This water moves as a coastal current from the Skagerak to the Barents Sea, whereas Atlantic water (with salinity above 35‰) moves northward farther offshore with the core just outside the edge of the continental shelf. The main bulk of coastal water seems to be deflected northward off Stad (Fig. 9), and outside Møre the current has its maximum northward velocity at the edge of the shelf, whereas over the Møre plateau the current is weaker and on some occasions vortex movements of the water masses occur (HELLAND-HANSEN and NANSEN 1909, LJØEN and NAKKEN 1969). The branch of the coastal water which follows the slope northwards from about N 63°15′, E 5°40′ is mixed with salter and warmer water masses and will relatively soon lose its original characteristics (LJØEN and NAKKEN 1969). The main bulk of coastal water flows to the east off Ona–Grip and follows the coast northwards from Grip (Fig. 9).

The velocity of the coastal current varies greatly (HELLAND-HANSEN and NANSEN 1909, EGGVIN 1940, LJØEN 1962). The subsurface drogue

Table 11. Subsurface drogue measurements in larval patches during the surveys in 1963–1965 and 1967.

Date		Drift station no.	Position	Duration of experiment in hours	Drifting velocity parallel to the coast in knots
1963	20–21.4	1	N 63° 44′, E 07° 52′	24	0.75
1964	18–19.4	2	N 65° 26′, E 10° 45′	24	1.08
	30.4	3	N 66° 33′, E 12° 02′	12	0.36
	28–29.4	4	N 68° 20′, E 13° 14′	24	0.29
1965	9–10.4	5	N 64° 20′, E 09° 32′	24	1.00
1967	3– 9.4	6	N 63° 06′, E 05° 51′	138	0.10 clockwise drift

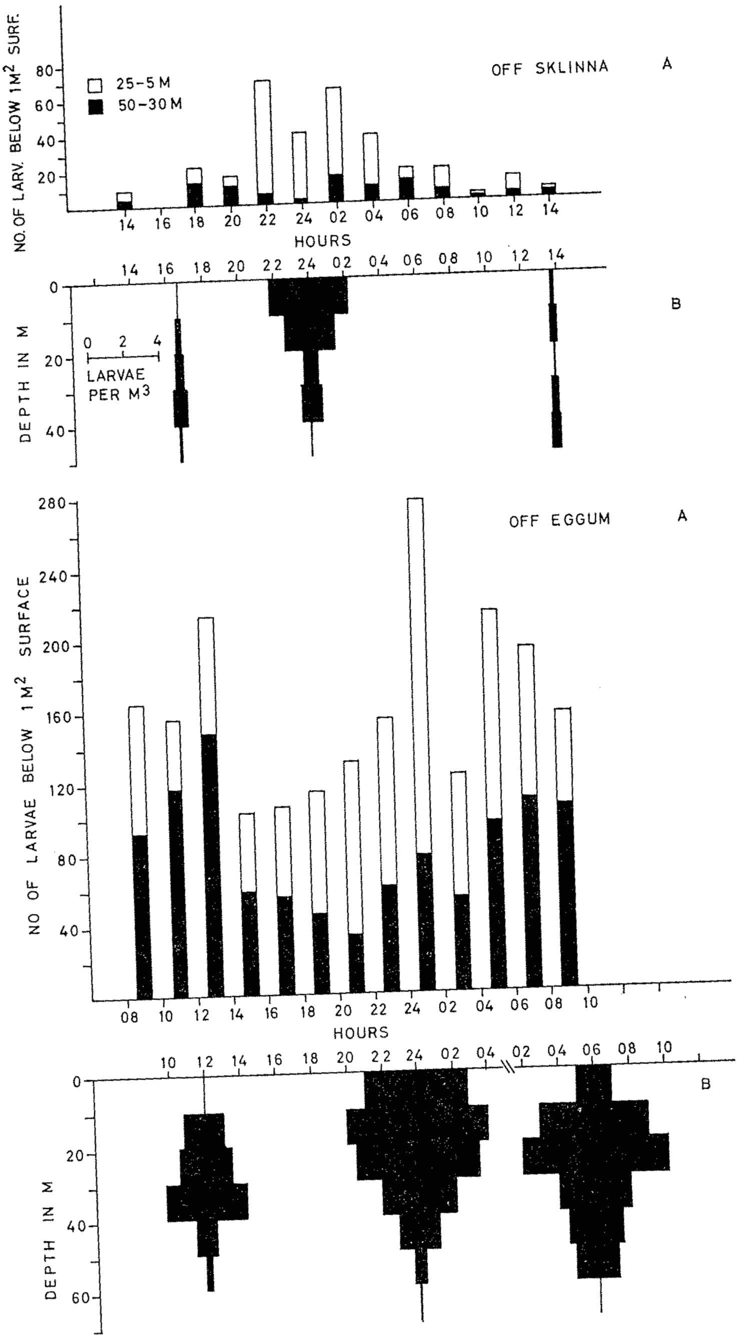

Fig. 8. (A) quantity of larvae caught in oblique hauls with CBPS during the survey in 1964 at drift stations 2 and 4 (off Sklinna and Eggum) during a 24-hour sampling period and (B) vertical distribution of larvae at the same stations.

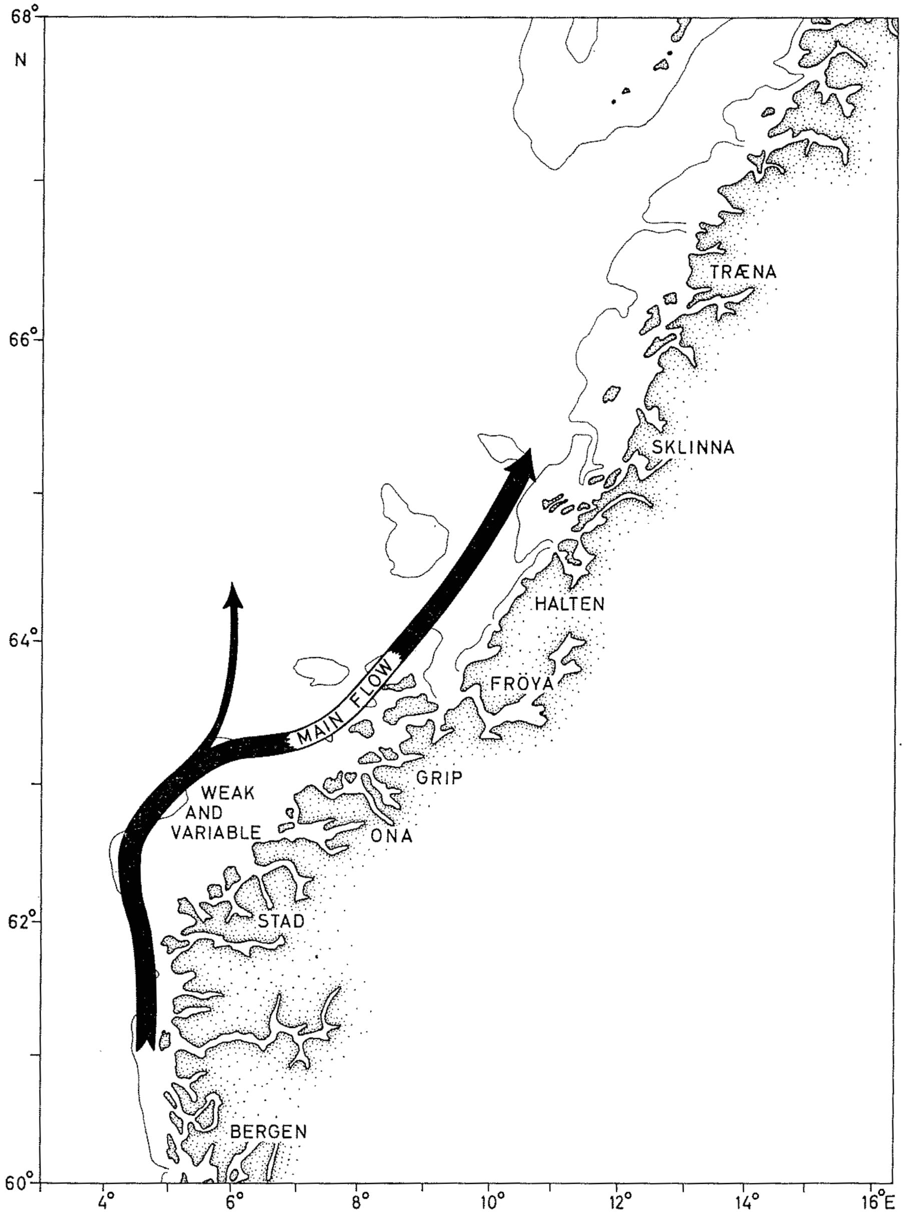

Fig. 9. Main flow of coastal water off Møre and Trøndelag (reconstructed from LJØEN and NAKKEN 1969).

measurements carried out at different places along the coast (Table 11) showed relatively high velocities off Frøya and Sklinna (stations 1, 2 and 5) and lower velocities farther north off Træna and Eggum (stations 3 and

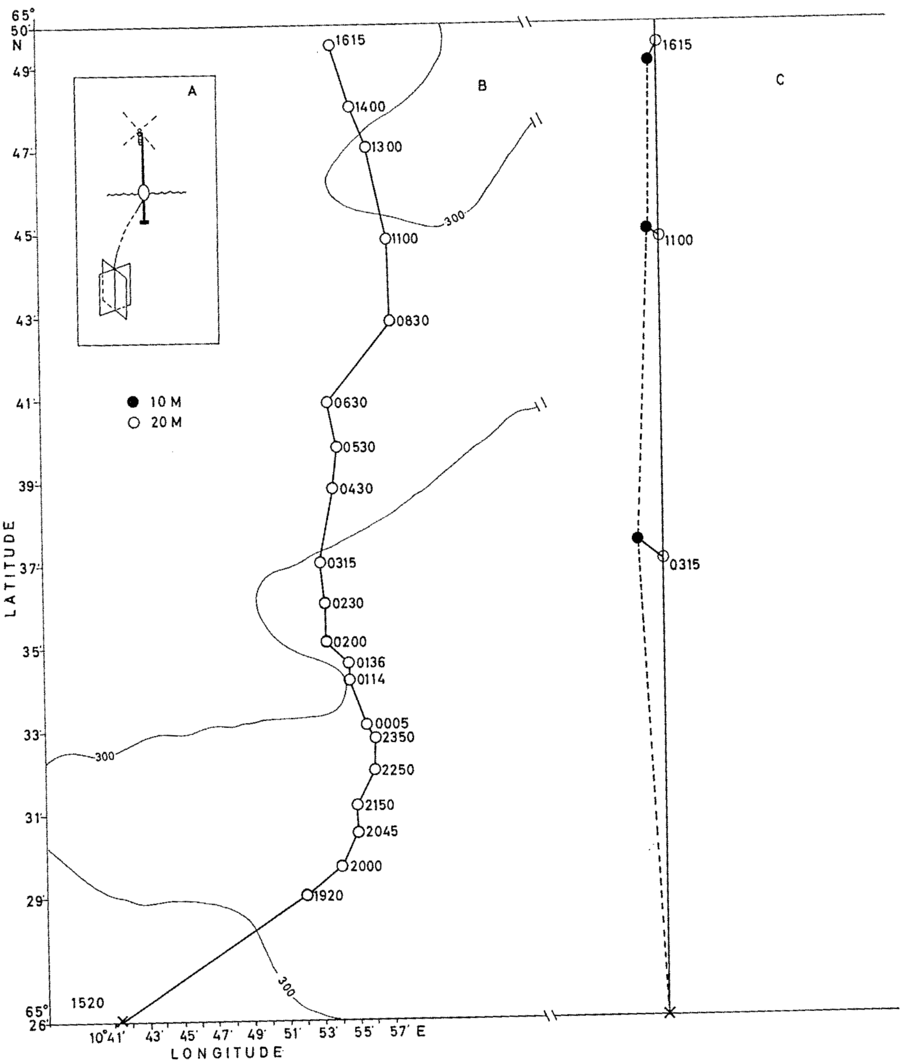

Fig. 10. (A) subsurface drogue, not drawn to scale, (B) drift path of a drogue at 20 m depth off Sklinna in 1964, from 18 April at 1520 hours to 19 April at 1615 hours (local time) and (C) positions of the drogue at 20 m depth compared with positions of drogue at 10 m depth.

4). On the shelf off Ona (station 6) a vortex movement took place during an experiment in 1967 (DRAGESUND and NAKKEN 1968). Thus the larval distribution and drift will vary depending on the location of spawning.

No important difference in the direction and velocity of the current was found between 10 and 20 m during the 1964 experiments (Fig. 10), and none was found between 10 and 40 m in an experiment carried out in 1965 (DRAGESUND and HOGNESTAD 1966).

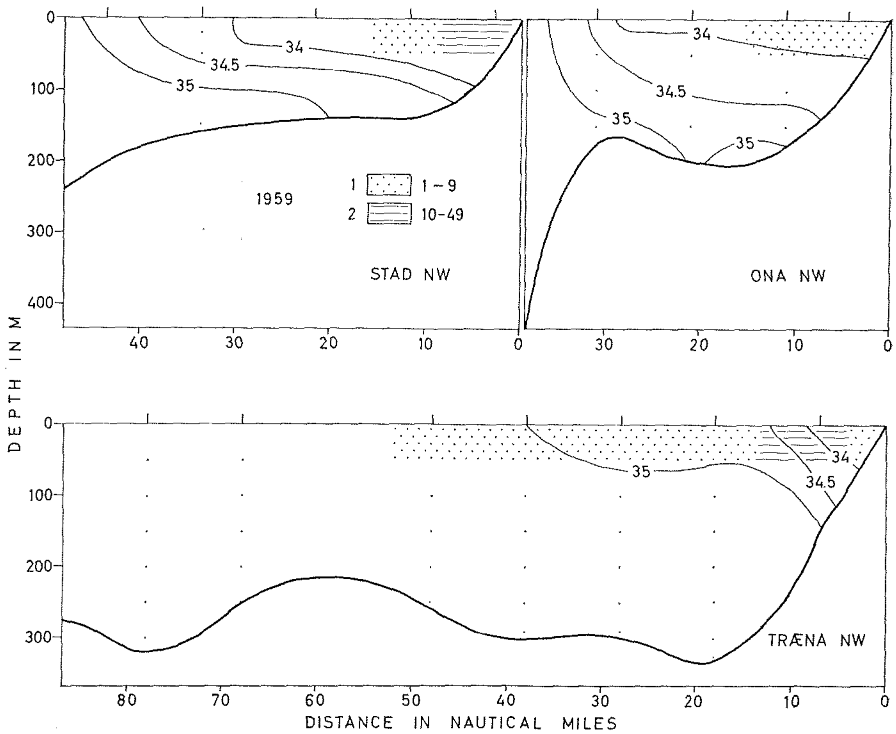

Fig. 11. Distribution of salinity (‰) in three vertical sections seaward from Stad, Ona and Træna, (1) and (2) number of larvae below 1 m² surface.

The seaward extent of larval distribution in 1959 in relation to the salinity distribution is shown in Fig. 11. All larvae in the two southernmost sections (off Stad and Ona) were found in coastal water, whereas farther north (off Træna) they were more dispersed and found also in Atlantic water. However, the most dense concentrations were observed in the core of coastal water where the main transport of larvae took place. The 35‰ isohaline at 0 m in relation to the larval distribution on the shelf between Stad and Lofoten is shown in Fig. 12.

Figs. 12–18 show the larval distribution in 1959–1965 during successive periods. The first survey in 1960 is not included as it was carried out prior to the time of main hatching (Fig. 7). In 1964 the first survey was omitted because sampling was made only at a few stations. The second survey of that year covered a relatively late period in relation to hatching in areas 07 and 06, but about the same period as in other years in area 05.

During the first annual survey period (Figs. 12–18A) the main larval concentrations from the spawning grounds in areas 07 and 06 were found between Stad and Sklinna, extending to the southernmost part of area

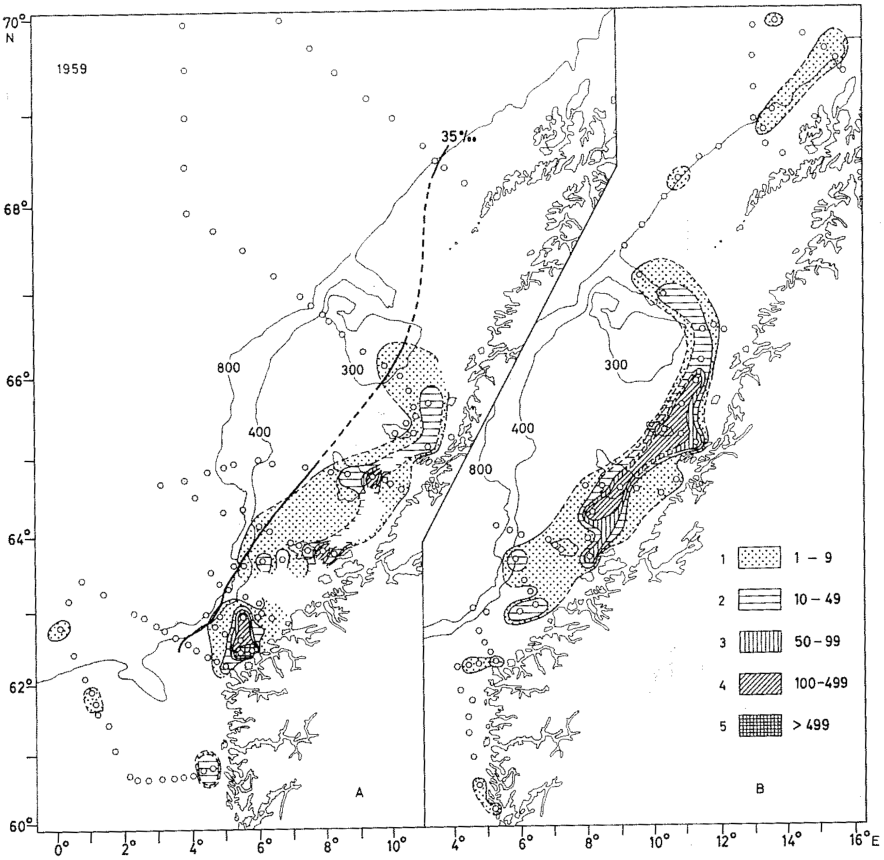

Fig. 12. Distribution of herring larvae in 1959, (A) all length groups (caught with Nansen net), 2–13 April, and the 35‰ isohaline at 0 m, (B) larvae ≥12 mm (caught with CBPS), 20–28 April. (1) to (5) number of larvae below 1 m^2 surface. Stations are plotted as circles.

07 in 1959–1961. In 1959, 1961, 1963 and 1964 the distribution in areas 07 and 06 was somewhat more wide than in 1962 and 1965. The distribution pattern was characterized by high larval concentrations near the coast, decreasing seaward and almost no larvae were found outside the edge of the shelf. In the years 1962–1965 larvae were scarce south of Ona, a result of the restricted spawning on the southern grounds.

In 1964 and 1965 the distribution was characterized by two main centres, one off the Møre–Trøndelag coast and the other off the coast between Træna and Eggum. In 1964 larvae from the spawning grounds off Møre (area 07) and Trøndelag (area 06) had already mixed with those from the Lofoten spawning grounds (area 05) when the survey was carried out, whereas in 1965 the larvae from the spawning off Møre–

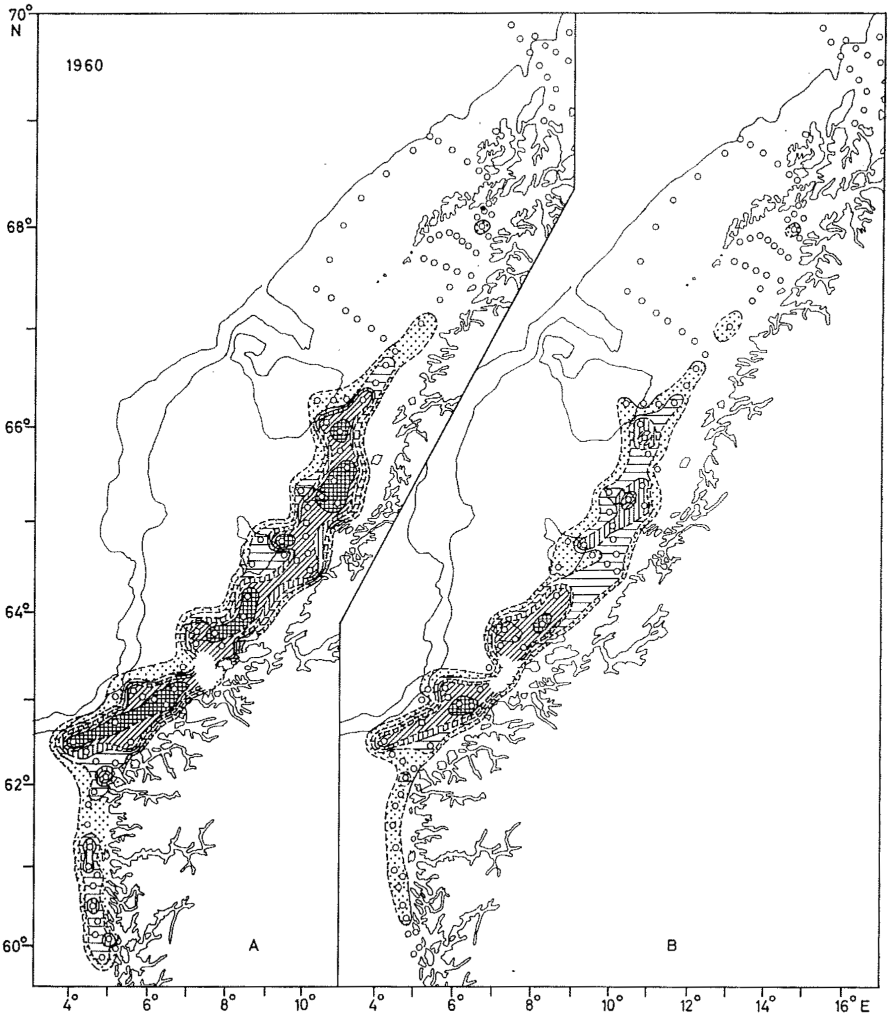

Fig. 13. Distribution of herring larvae 31 March–9 April 1960, (A) all length groups and (B) ≥12 mm. Legend as in Fig. 12.

Trøndelag were separated from those hatched at Lofoten. During April of 1964 and 1965 the major part of the larval population was located farther north than at the same time in earlier years (1959–1961), mainly because of the spawning at Lofoten.

In general the abundance of larvae was high during or immediately after the time of the main hatching, especially in 1960 (Fig. 19A). In 1962 and 1965 high catches were restricted to a limited region off Frøya, whereas in 1963 and 1964 relatively low catches were obtained at all sections (1959 is omitted due to lack of data with CBPS). In 1967 evidence

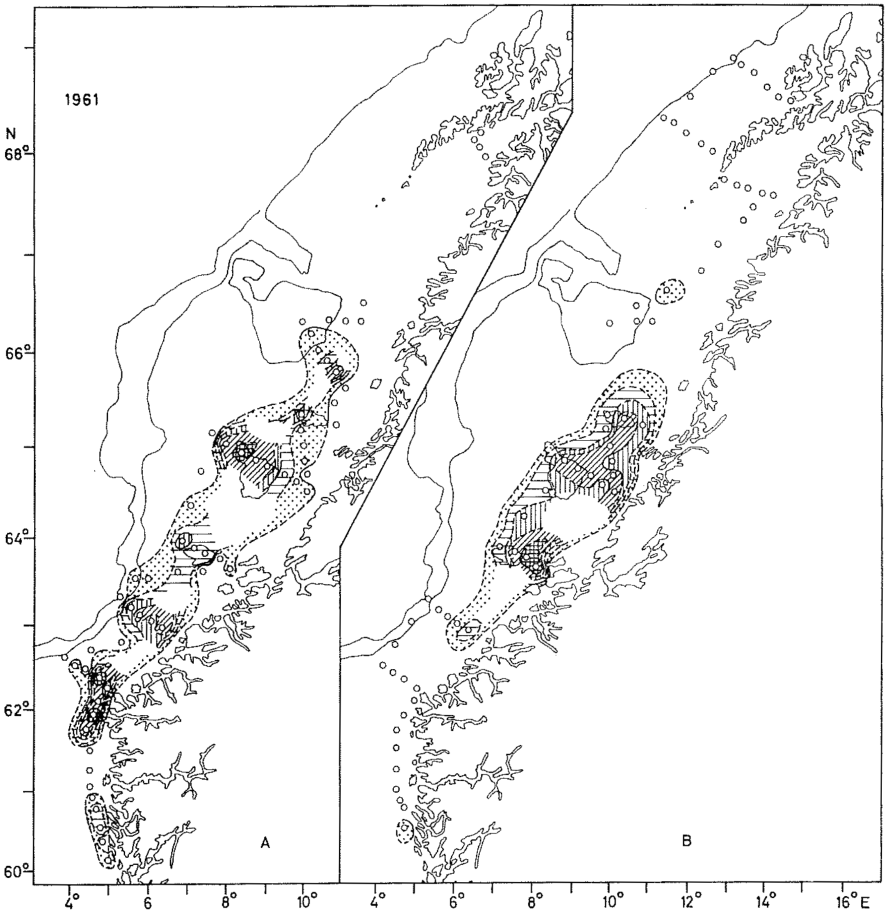

Fig. 14. Distribution of herring larvae in 1961, (A) all length groups, 6–19 April and (B) ≥12 mm, 20–29 April. Legend as in Fig. 12.

of a mass mortality of larvae off Møre soon after hatching (i.e. during the growth period between 10 and 12 mm of length) was found by DRAGESUND and NAKKEN (1968). When comparing the distribution and abundance of larvae in relation to subsequent year-class strength, therefore, those having passed the yolk sac stage (i.e. larvae ≥12 mm) should be considered separately.

In Figs. 12–18B the distribution of these larvae are shown during the second annual survey period. In 1961, 1962 and 1965 the post yolk sac larvae were concentrated off Frøya and were considerably less abundant south and north of this region. In 1961 larvae also were numerous off Halten. In 1959, 1960, 1963 and 1964 the larvae were more widely distributed. Because of the variable sampling time in relation to hatching, it

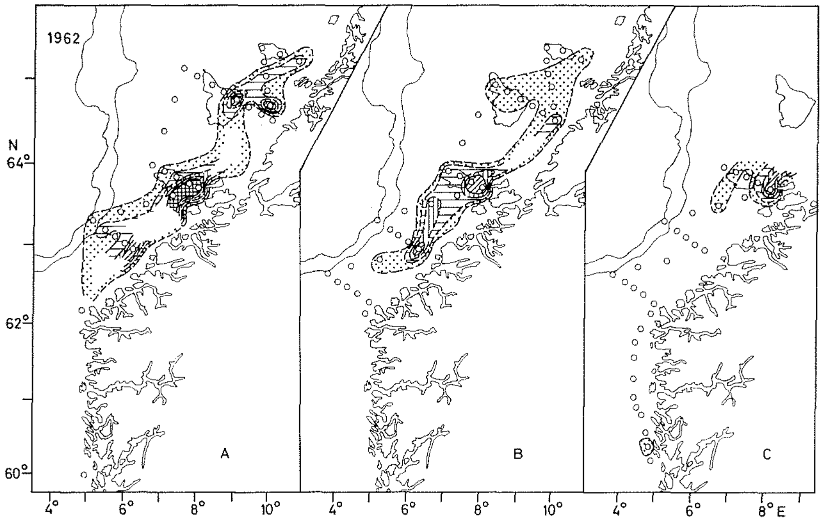

Fig. 15. Distribution of herring larvae in 1962, (A) all length groups, 2–9 April, (B) ≥12 mm, 6–13 April and (C) ≥12 mm, 24–28 April. Legend as in Fig. 12.

is difficult to make a quantitative comparison of the abundance estimates between years. Table 12 shows the percentage of larvae ≥12 mm and of larvae ≥15 mm during the second period of sampling. In 1959 96.3% of the larvae were ≥12 mm, whereas the corresponding figures for the following years were considerably lower, particularly in 1960. Larvae hatched off Lofoten were mainly below 12 mm in length at the time of sampling.

Table 12. Percentage of larvae ≥12 mm and ≥15 mm during the second annual sampling period for each of the years 1959–1965.

Date		Area	No. of stations	Total no. of larvae below 1 m^2 surface	≥12 mm	≥15 mm
1959	23–28.4	07 and 06	30	1435	96.3	53.0
	20–23.4	05	8	31	87.1	45.2
1960	2– 8.4	07 and 06	59	26445	21.9	0.0
	28.3– 2.4	05	2	9	0.0	0.0
1961	21–29.4	07 and 06	22	4824	84.1	13.6
1962	24–27.4	07 and 06	8	1047	32.9	2.7
1963	16–23.4	07 and 06	38	1809	66.1	2.5
	13–16.4	05	3	18	16.7	16.7
1964	13–20.4	07 and 06	34	1224	59.2	30.4
	20–30.4	05	51	3375	29.4	7.1
1965	7–12.4	07 and 06	27	2127	57.3	5.6
	4– 7.4	05	15	443	24.4	0.0

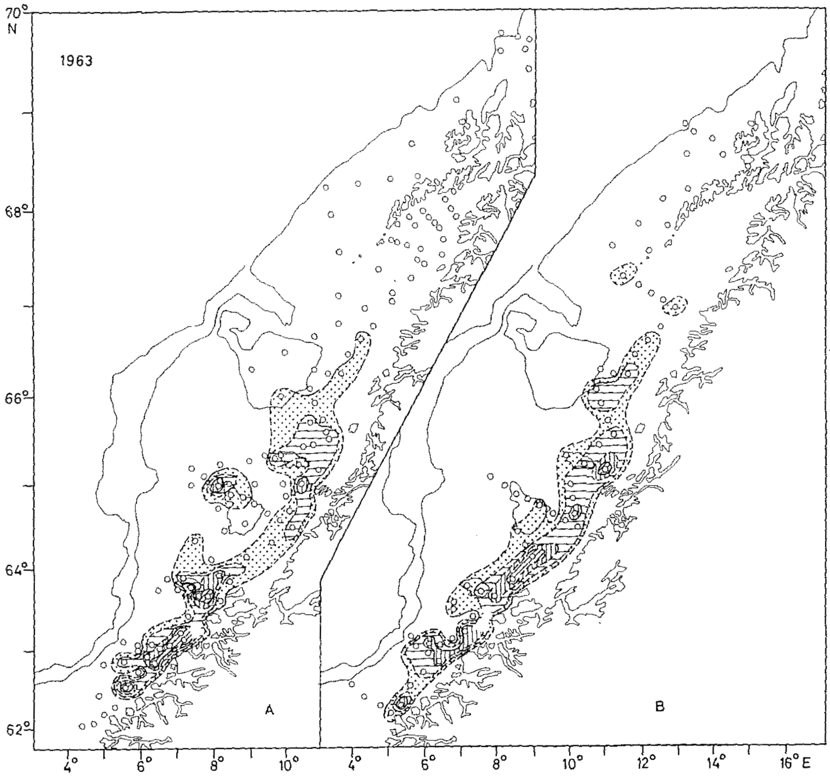

Fig. 16. Distribution of herring larvae in 1963, (A) all length groups, 2–10 April and (B) ≥12 mm, 13–23 April. Legend as in Fig. 12.

The number of larvae ≥12 mm and ≥15 mm per station at the sections off Stad, Ona, Frøya, Halten, Sklinna and Træna is illustrated in Fig. 19B (1960 is omitted). Less variable values were found at the different sections for post yolk sac larvae ≥12 mm in 1959, 1963 and 1964 than in 1962 and 1965. In 1961 a marked displacement northward had taken place between the two sampling periods, and the larvae were evidently more concentrated during the second than during the first period of sampling. The abundance off Frøya and Halten in 1961 was markedly higher than in the other years. The number of larvae ≥15 mm was low except for 1959 and 1961. More than 50% of the larvae caught in 1959 were ≥15 mm. This may have resulted in an underestimate of the abundance of the 1959 larvae compared with other years as the catching efficiency of CBPS is lower for larger than smaller larvae. Mortality from hatching up to the sampling stage adds also to this underestimate.

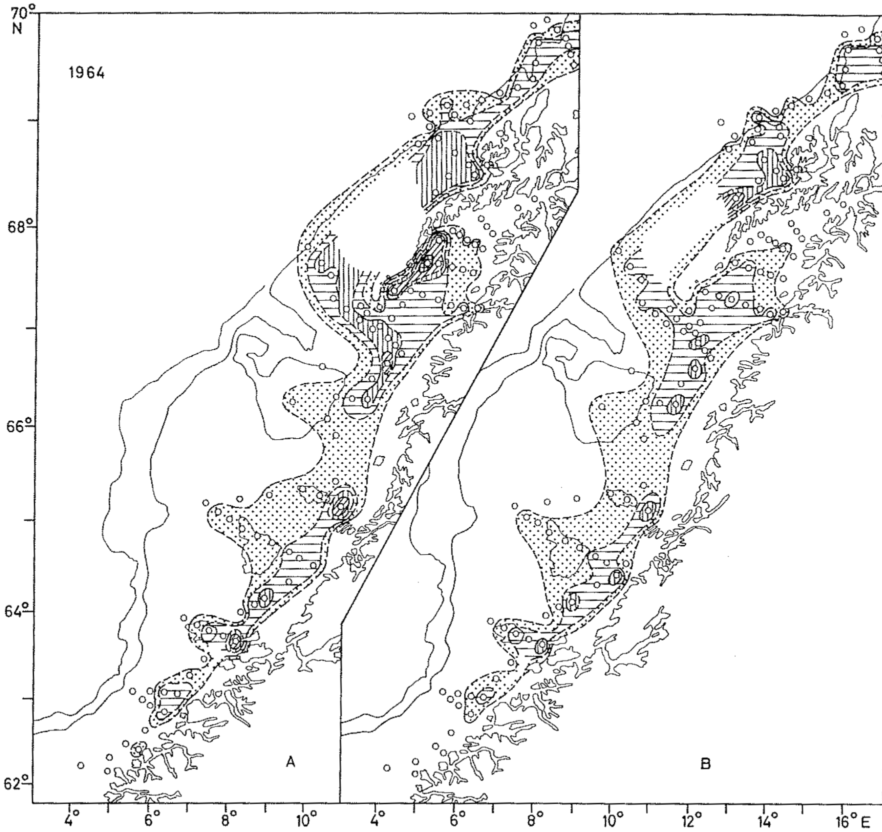

Fig. 17. Distribution of herring larvae 13–18 April 1964, (A) all length groups and (B) ≥12 mm. Legend as in Fig. 12.

The following characteristic features of the distribution and abundance of the larvae can be listed:

1) the abundance was relatively high during the post yolk sac stage in 1959;

2) the highest abundance just after hatching was found in 1960, and the exceptionally high figures found at all sections that year indicated a high hatching success over a wide spawning area;

3) the 1961 larvae were also numerous after hatching and throughout the post yolk sac stage, though more marked concentrated during the second than during the first period of sampling;

4) the 1962 and 1965 larvae were more concentrated and had a more patchy distribution than in other years;

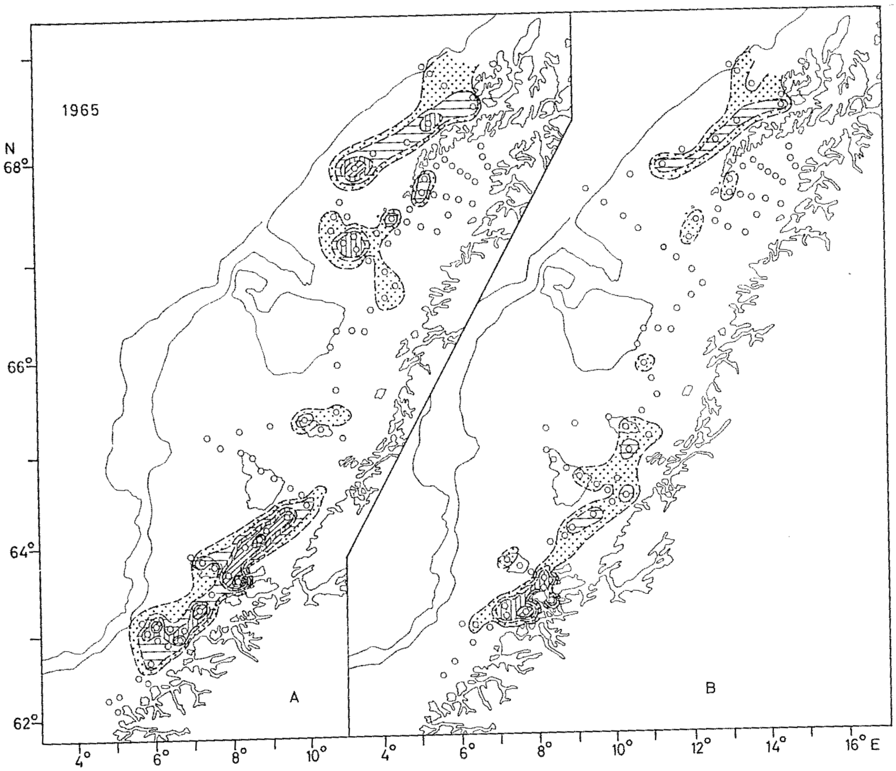

Fig. 18. Distribution of herring larvae in 1965, (A) all length groups, 29 March–6 April and (B) ≥12 mm, 4–12 April. Legend as in Fig. 12.

5) the distribution in 1963 and 1964 was widespread, particularly during the second period of sampling, but the abundance at the different sections were low;

6) the abundance estimates at the different sections between Stad and Træna suggest that the variation in the size of the spawning stock was reflected in the larval abundance figures obtained in the period just after hatching.

As indicated by the distribution charts (Figs. 12–18) a northward displacement of the larval concentrations in the southern part of the survey area was observed in most of the years. In the northern part of the area time intervals between surveys were too short to allow any marked northward drift to be recorded. However, in 1959 a displacement northward off Træna was traced. To illustrate the drift from a known spawning site near Grip, the larval distributions during two successive periods of the survey in 1968 are shown (Fig. 20). The spawning site was located on

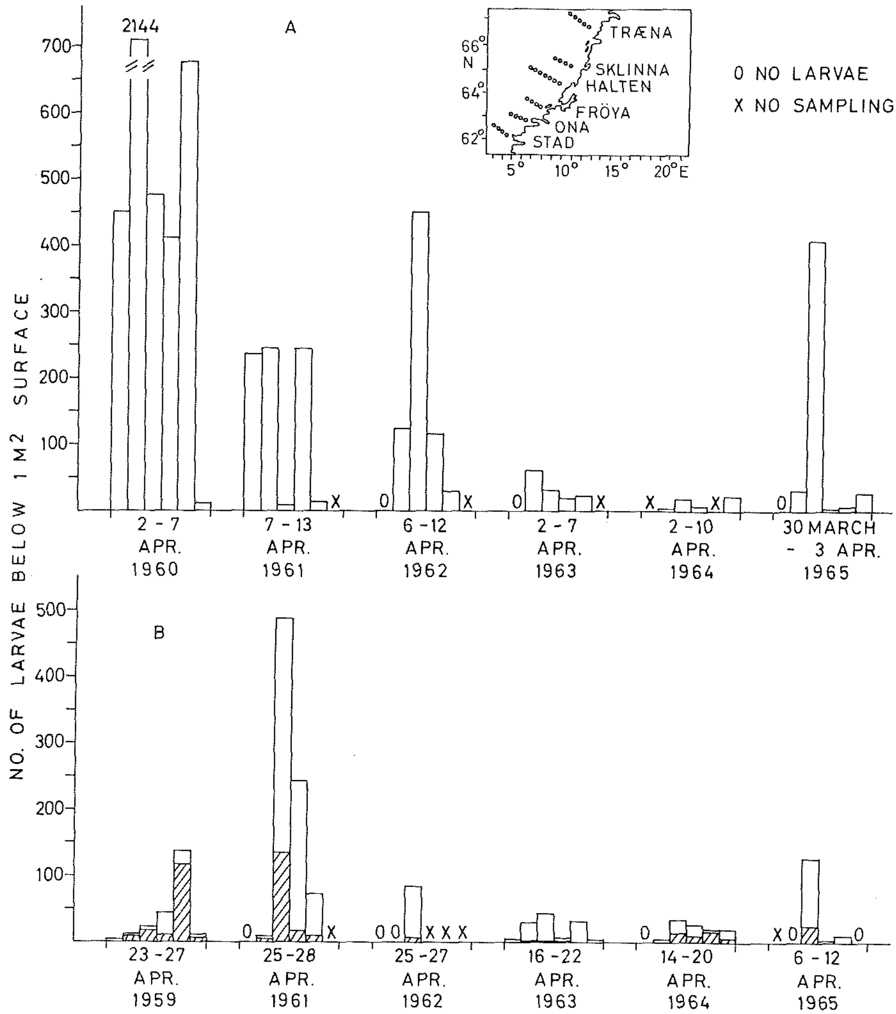

Fig. 19. Number of larvae below 1 m^2 of surface per station at six sections, from left to right: Stad, Ona, Frøya, Halten, Sklinna and Træna, (A) larvae of all length groups, (B) of larvae ≥ 12 mm and ≥ 15 mm (diagonal shading).

23 March when eggs were collected with dredge. Adult herring were recorded near the bottom some days earlier at the same locality. The eggs were examined and fertilization was estimated to have taken place from 5 to 10 March. Further inspections were carried out from 25 to 31 March, and the larvae were now nearly at the hatching stage. A detailed sampling programme was started, and during the following few days larvae were numerous just north of the spawning site. Assuming that the majority of the larvae were derived from this spawning site, the drift was

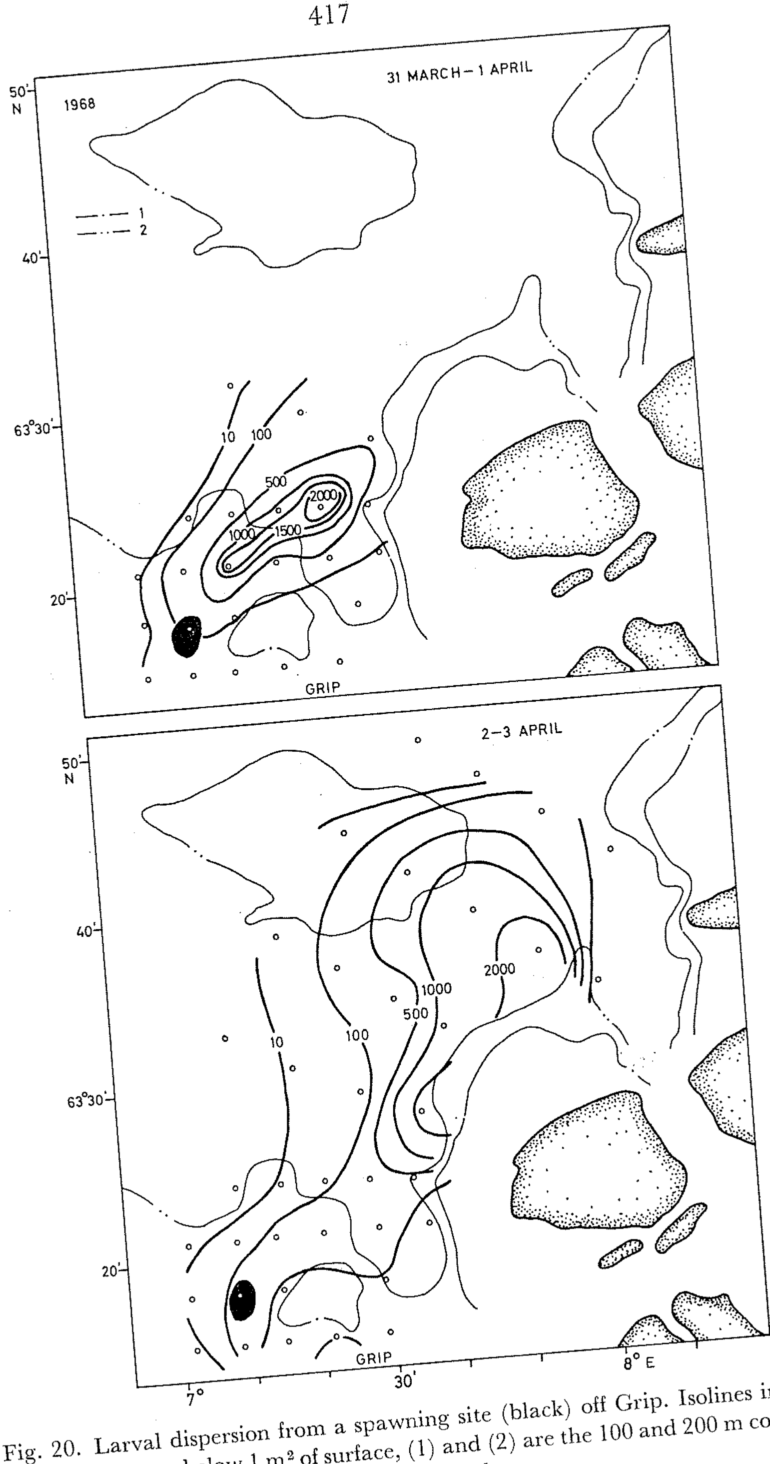

Fig. 20. Larval dispersion from a spawning site (black) off Grip. Isolines indicate the number of larvae below 1 m^2 of surface, (1) and (2) are the 100 and 200 m contour lines, respectively.

estimated to 0.67 knots by measuring the distance between the centres of concentrations in two successive sampling periods. The estimated drifting velocity was slightly lower than indicated by the subsurface drogue measurements farther north off Frøya and Sklinna in 1963–1965 (Table 11).

Since the larvae are mainly found in the upper 50 m, it may be assumed that the force and direction of the wind play an important role in determining the distribution pattern of larvae. Although the coastal current is directed northward, the surface water may be turned in various directions by the wind force. In periods with southerly winds the larvae will be transported northwards relatively quickly, whereas the drift will be hampered when winds from north prevails as the wind produces not only a pure wind current to the right of the wind direction, but also a relative current that runs parallel to the coast (EKMAN 1923, SVERDRUP, JOHNSON and FLEMING 1946). Therefore, wind data from the meteorological stations Ona, Nordøyane and Skomvær have been analysed (Fig. 21).

The wind distribution in 1961 presumably resulted in a rather strong northward flow of water in the southern area but a weak northward flow in the northern area. In 1962 the same trend was found, although the wind vectors were smaller. In these years the wind distribution thus may have hampered the northward drift of the larvae from the spawning region in area 06, and may also partly have accounted for the high concentrations of larvae found between Frøya and Halten. For 1959, 1960, 1963 and 1964 the wind vectors indicate a prevailing strong northward flow of water resulting in more widespread north–south distribution of larvae.

The larval drift also may be studied in relation to the distribution of recovered drift bottles released in larval patches at various places during the surveys in 1961 and 1963–1965 (Fig. 22). All the bottles recovered in 1961 were found within thirty days after release in the coastal belt, and the high frequency of returns indicates that they were transported northwards close to shore. The 1963 recoveries showed a quite different distribution. None of the bottles released was recaptured within thirty days, and all the returns are from areas farther north (areas 05, 04 and 03). This distribution indicates that the bottles drifted northwards at some distance from the coast during the first period after release. Bottles released in 1964 and 1965 in area 07 were frequently recovered in areas 07 and 06, indicating a drift nearer to the coast in those years. Bottles recovered within sixty days in 1964 were distributed somewhat farther north than in 1965, indicating a faster drift in 1964. The drift of bottles along the coast from Møre to Finnmark was clearly demonstrated, and it is likely that larvae hatched off Møre are transported to this area.

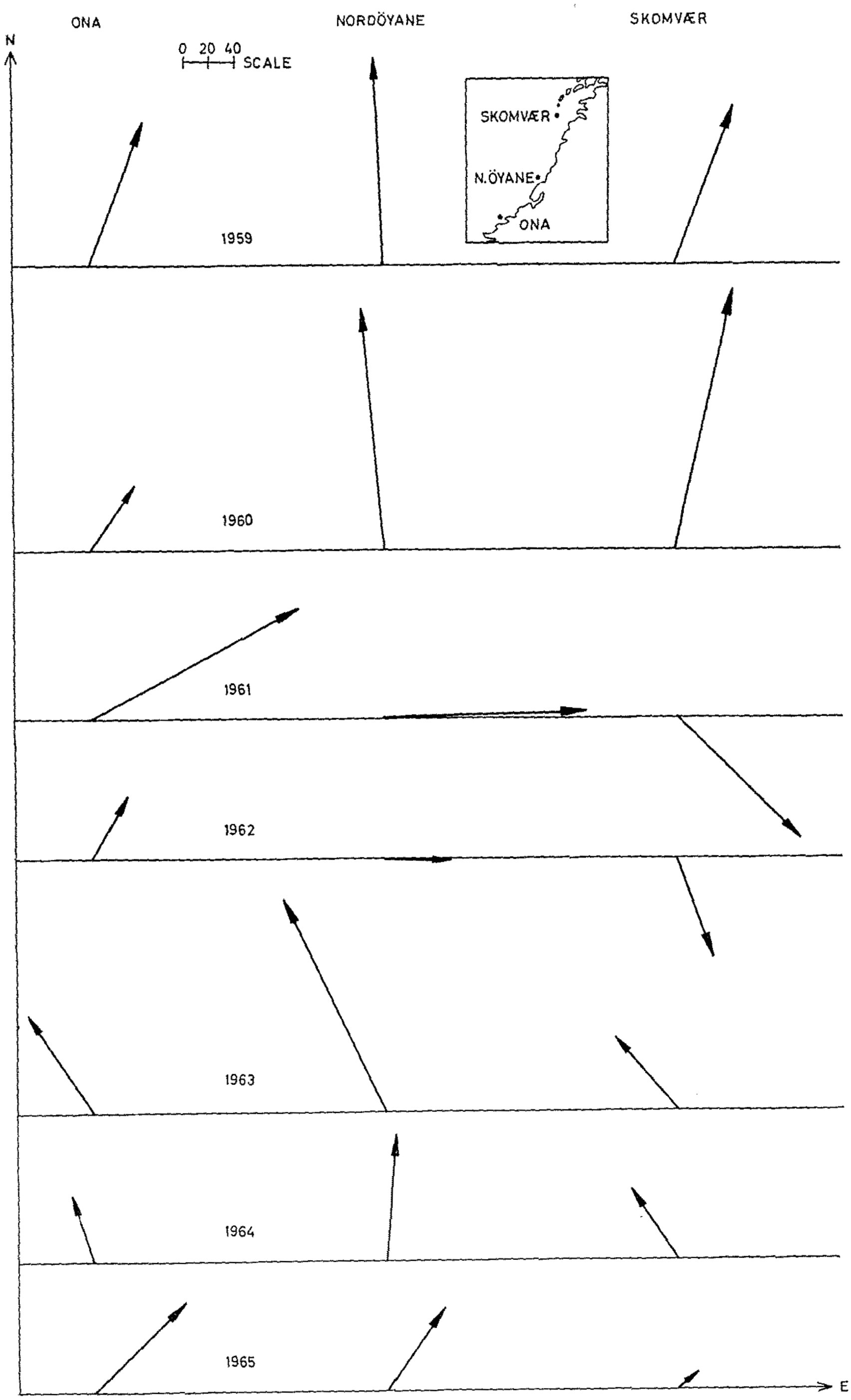

Fig. 21. Average resultant wind vectors for the period March–April in 1959–1965.

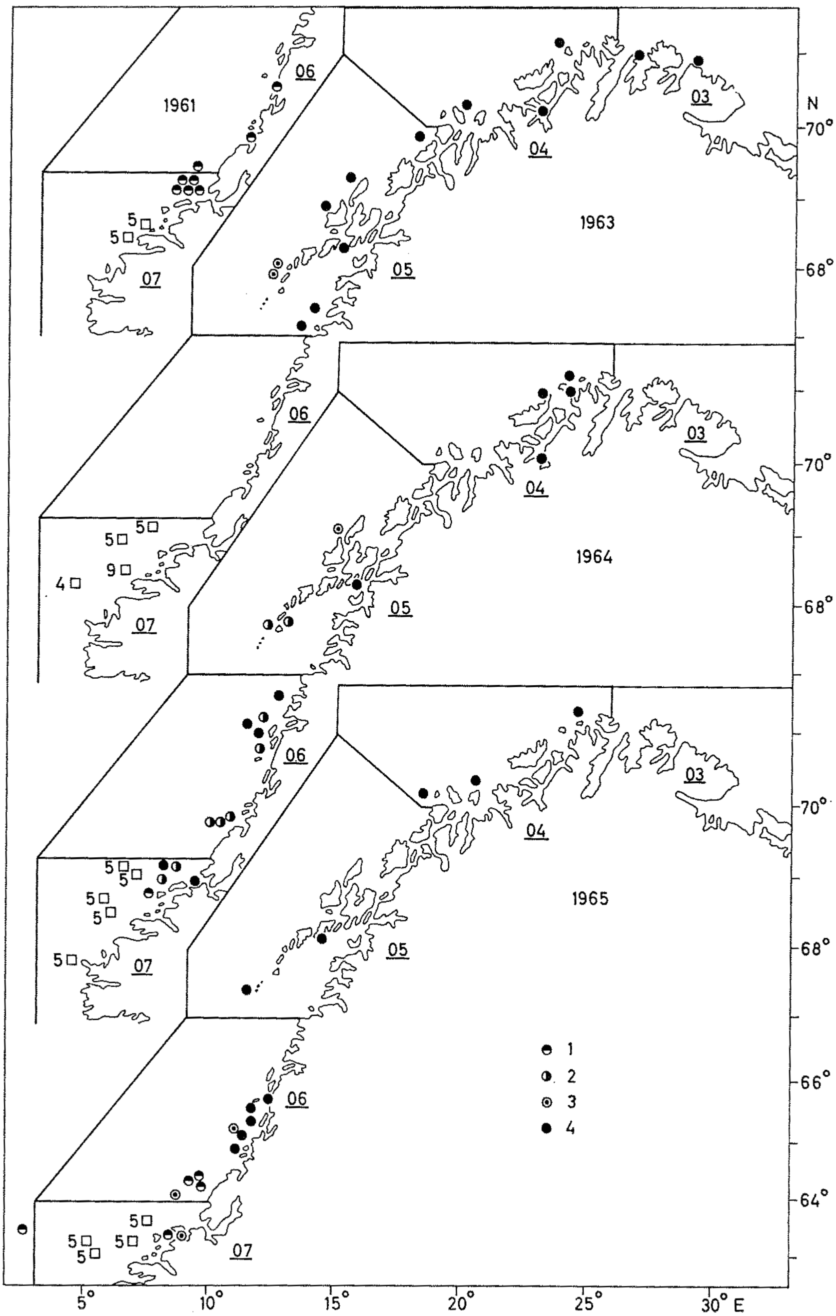

Fig. 22. Drift bottle experiments in 1961 and in 1963–1965. Open squares denote positions of releases and circles distribution of recoveries, (1) within 30 days, (2) between 31 and 60 days, (3) between 61 and 90 days and (4) more than 90 days after release. The number of drift bottles released at each position is listed in the figure.

The general drift pattern of larvae can be summarized as follows:

1) an extensive northward drift of larvae takes place from all the spawning grounds along the coast;
2) larvae hatched south of Stad will probably be transported northward near the coast, but a more offshore distribution is possible when they pass the region off Møre;
3) larvae drifting northward along the coast may follow a vortex movement over the southern part of the Møre plateau;
4) larvae being transported offshore will most likely be deflected towards the coast again off Grip–Frøya where the northward flow is relatively rapid before it slows down again off the coast between Træna and Lofoten;
5) during the northward drift part of the total larval population will accumulate at the entrance of the fjords along the Norwegian coast, and this part is probably greatest when the spawning takes place in the southernmost region (within area 08).

LARVAL LENGTH IN RELATION TO TIME OF SPAWNING

The length distribution of larvae in different regions between Bergen and Andenes is shown in Figs. 23 and 24. During the first period of sampling in 1959–1961 larger modal lengths were found between Stad–Ona and Grip–Frøya than south and north of these regions. It is assumed, therefore, that spawning started in the central part of the main spawning district (i.e. between Stad and Ona), and that the onset of spawning occurred slightly later to the south and north of this area. In 1962–1964 the largest modal lengths were found off Grip–Frøya, indicating that spawning started first between Ona and Grip. However, in 1962 only small differences in lengths were found in relation to both region and time. The late onset and the restricted duration of spawning that year presumably led to a mass spawning over a relatively short period resulting in smaller variations in lengths. Similarly, no marked trends were found in the length distributions of larvae between Stad and Halten in 1965. This suggests simultaneously hatching on all spawning grounds.

Table 13 lists the coefficients of variation (v) for the different length distributions

$$v = \frac{s}{\bar{l}} 100$$

where s is the standard deviation and $\bar{l}$ the mean length.

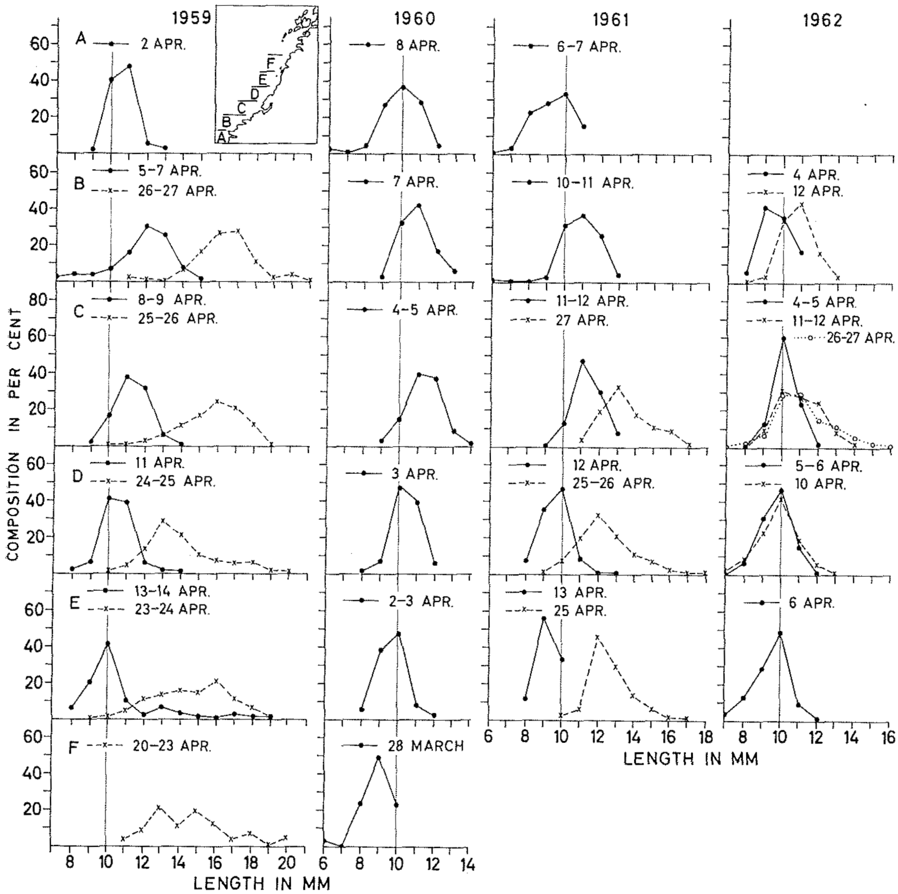

Fig. 23. Length distribution of larvae caught with CBPS in 1959–1962, (A) Bergen-Kinn, (B) Stad-Ona, (C) Grip-Frøya, (D) Halten, (E) Sklinna and (F) Træna. Data on larval lengths from CBPS and Nansen net are pooled for the second part of the 1959 survey (20–27 April). Prior to this period the larvae were caught with Nansen net.

The coefficients were relatively high in 1959, reflecting the long duration and low rate of spawning (Table 10). Although the spawning seasons were long, the coefficients of variation for 1960 and 1961 were lower than for 1959, suggesting that the main hatching was concentrated over a shorter period these years. This is also supported by the relatively high spawning rate and the high numbers of larvae per station in 1960 and 1961 (Fig. 19).

In 1964 the length distributions were bimodal in most of the regions during the second period of sampling, probably because of the difference in spawning time between the spawning regions off Møre–Trøndelag and off Lofoten and also within the Møre–Trøndelag spawning regions. The

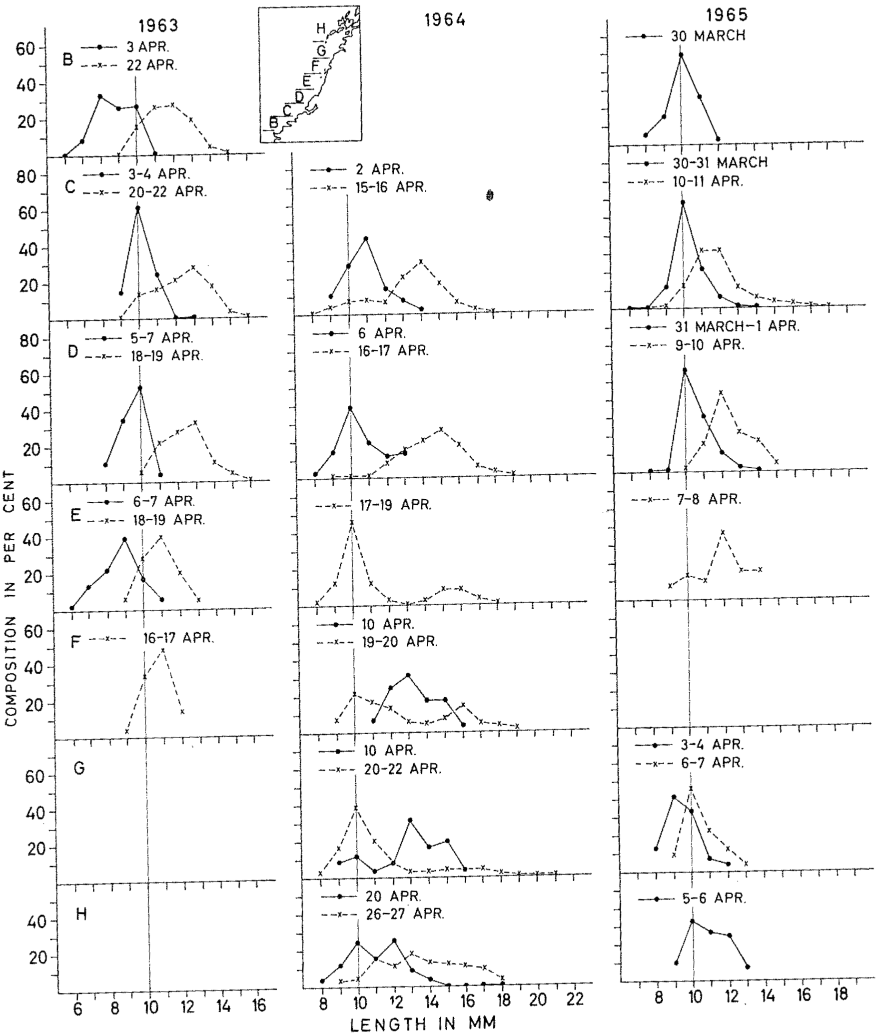

Fig. 24. Length distribution of larvae caught with CBPS in 1963–1965, (B) Stad-Ona, (C) Grip-Frøya, (D) Halten, (E) Sklinna, (F) Træna, (G) Lofoten and (H) Eggum-Andenes.

age composition of the spawners may explain the differences in spawning time between and within the regions, the recruits spawning later in the season than repeat spawners. The largest larvae found in area 06 may have been produced by old fish which spawned relatively early in the season, whereas the smaller larvae probably originated from recruits which spawned slightly later. The larger larvae caught between Lofoten and Andenes were most likely transported from spawning grounds south of this region.

Table 13. Coefficients of variation (v) for larvae caught in different regions between Bergen and Andenes during the larval surveys in 1959–1965.

Region	1959			1960			1961		
	Date	No.	v	Date	No.	v	Date	No.	v
Bergen-Kinn	2.4	39	7.1	8.4	122	9.8	6–7.4	129	11.6
	28.4	8	14.3	—	—	—	—	—	—
Stad-Ona	5–7.4	443	14.1	23.3	114	13.1	10–11.4	245	8.6
	26–27.4	101	10.7	7.4	499	7.8	28.4	22	6.1
Grip-Frøya	8–9.4	141	8.6	23.3	294	8.8	11–12.4	383	7.5
	25–26.4	139	10.8	4–5.4	400	7.5	27.4	630	10.0
Halten	11.4	120	9.7	24.3	38	—	12.4	254	8.0
	24–25.4	133	14.4	3.4	148	7.0	25–26.4	1074	12.0
Sklinna	13–14.4	65	22.4	25.3	123	7.7	13.4	142	6.7
	23–24.4	450	14.0	2–3.4	400	6.9	25.4	344	8.4
Træna	20–23.4	65	14.8	28.3	55	9.1	—	—	—
	1962			1963					
Stad-Ona	4.4	53	8.8	3.4	175	11.4			
	12.4	378	8.2	8.4	29	7.3			
	—	—	—	22.4	161	10.3			
Grip-Frøya	4–5.4	1339	6.5	3–4.4	271	6.1			
	11–12.4	1129	11.1	7–8.4	266	7.6			
	26–27.4	674	13.4	20–22.4	341	11.8			
Halten	5–6.4	509	9.1	5–7.4	50	7.7			
	10.4	480	10.9	18–19.4	190	9.8			
Sklinna	6.4	277	9.7	6–7.4	139	11.3			
	—	—	—	18–19.4	139	8.2			
Træna	—	—	—	16–17.4	56	6.6			
	1964			1965					
Stad-Ona	—	—	—	30.3	38	8.7			
	—	—	—	—	—	—			
	—	—	—	—	—	—			
Grip-Frøya	2.4	46	10.1	30–31.3	1419	7.7			
	15–16.4	110	14.6	10–11.4	756	12.1			
Halten	6.4	42	12.3	31.3–1.4	835	7.6			
	16–17.4	107	6.3	9–10.4	56	9.0			
Sklinna	17–19.4	144	22.5	2.4	14	3.0			
	2.5	45	27.5	7–8.4	38	12.4			
Træna	10.4	29	9.9	—	—	—			
	19–20.4	185	21.2	—	—	—			
Lofoten	10.4	37	15.2	3–4.4	132	10.2			
	20–22.4	503	21.1	6–7.4	103	9.6			
	29–30.4	104	23.0	—	—	—			
Eggum-Andenes	20.4	84	18.0	5–6.4	110	10.2			
	26–27.4	78	16.4	—	—	—			
	27–29.4	290	13.2	—	—	—			

Also the mixture of relatively young recruit spawners and old repeat spawners (off Møre and Trøndelag) may have contributed to the expanded bimodal length distribution of larvae. According to BLAXTER and HEMPEL (1963) and HEMPEL and BLAXTER (1967) young recruit spawners produce slightly smaller eggs and hence smaller larvae. The difference in egg weight between the youngest recruit spawners and the next age group in Norwegian herring was about 10–14%, so the difference in egg size and spawning date worked in the same direction and contributed to the bimodal length distribution of larvae.

No such bimodality in the length distribution was found in 1965 when both young recruits and old repeat spawners were present on the southern spawning grounds off Møre. However, the old fish made up only 15–20% of the stock in this region. In 1965 both the duration and the time of main spawning were nearly the same over the entire spawning area from Ona to Lofoten. This resulted in smaller length variations compared with 1964.

DISCUSSION

SPAWNING CHARACTERISTICS

The relationship between year-class strength and the following factors will be discussed:

1) age structure and size of the parent stock;
2) location of spawning;
3) duration and time of spawning.

The effect of the age structure of the parent stock on the year-class strength has been discussed by MARTI (1959) and BRIDGER (1961). They suggested that older herring produce bigger eggs resulting in stronger larvae with better yolk reserves. BLAXTER and HEMPEL (1963) found that the egg size and survival time on yolk reserves depend little on the age structure of the parent stock, although very young recruits produce slightly smaller eggs and larvae. Thus, in years when the stock consists mainly of very young spawners, the viability of the progeny may be reduced. During the 1950s young recruits were relatively abundant in 1954 (ØSTVEDT 1963). In the period 1959–1965 the influx of young recruit spawners was highest in 1964 and 1965, but also in 1963 recruits of the 1959 year-class appeared on the spawning grounds in significant numbers. The 1963 and 1964 year-classes were of average strength, whereas those of 1954 and 1965 were very poor (Fig. 25). From 1955 to 1962 repeat spawners and relatively old recruits dominated in the stock, and in most of these years poor year-classes were produced. Accordingly no apparent relationship can be established between the age structure of the parent stock and subsequent year-class strength.

In Fig. 25A the absolute size of the parent stocks for the period 1947–1962 is plotted against subsequent year-class strengths at six years of age. The absolute size of the spawning stocks during the period 1947–1952 has been derived from data given by ØSTVEDT (1963). The abundance indices showed that stock size remained at about the same level during this period, and was somewhat lower than that which occurred in the mid-1950s. The average abundance figure for the stock size during the period 1947–1952 was about 83% of the average figure for the years 1954–1956.

Estimates of year-class strength for adults are complicated by the wide range of ages over which individuals of a given year-class attain sexual maturity. However, knowing the size of the spawning stock, an estimate of year-class strength can be obtained by calculating the abundance of the year-class at an age when most of the year-class has entered the adult stock. According to ØSTVEDT (1958) the mean age at first spawning for herring of northern growth type (slowly growing herring) varies between 5.1 and 7.5 years, and for herring of southern growth type (rapidly growing herring) between 4.1 and 4.5 years. The strength of a year-class as adults, therefore, has been estimated at an age of six years (Fig. 25A).

During the period 1947–1962, two exceptionally rich year-classes were spawned, those of 1950 and 1959. The 1959 year-class was spawned when the adult stock was about half the size of that in 1950. During the period 1947–1956 the spawning stock was two to three times larger than in 1959, without producing any rich year-classes. In 1957 and 1958 the stock was also more abundant than in 1959, and again very poor year-classes occurred. The survival of the herring spawned in 1959 must have been relatively high since a rich year-class was spawned by a much smaller spawning stock than the stock which was present during the previous eight years. Similarly the survival was relatively high for herring spawned in 1960, although markedly lower than for those spawned in 1959. The 1962 year-class was very poor, being of the same magnitude as the year-classes spawned during the 1954–1958 period. The 1963–1965 year-classes had not reached the adult stage in 1968 and cannot be compared with the previous year-classes in the adult stock. Investigations carried out during the 0-group stage (DRAGESUND 1970) indicated that the 1963 and 1964 year-classes were slightly more abundant than that of 1961, whereas the 1965 year-class was very poor and probably less abundant than that of 1962 (Fig. 25B).

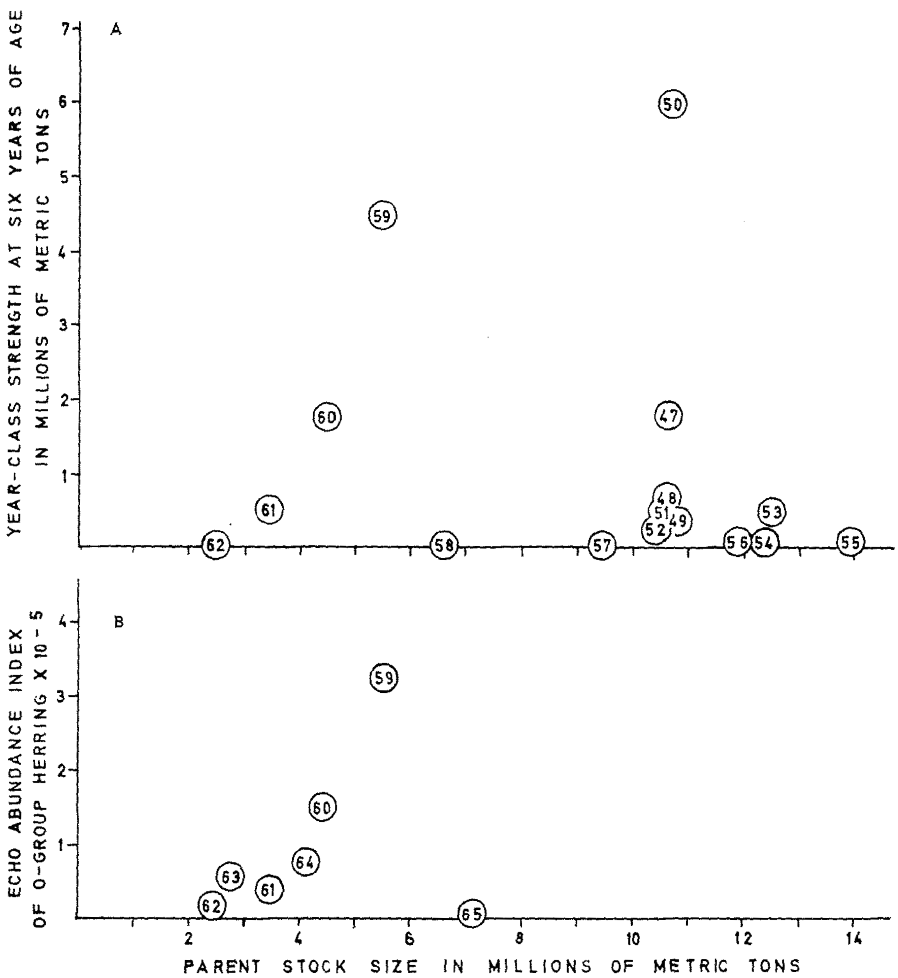

Fig. 25. Relationship between the parent stock size and the subsequent year-class strength, (A) at six years of age for the 1947–1962 year-classes and (B) at about six months of age for the 1959–1965 year-classes. The respective year-classes are indicated inside each circle.

The correlation diagram suggests that within the period considered, a relationship existed between the stock and the abundance of the resulting year-class when conditions for the progeny were favourable. However, in most of the years year-class strength was determined by other factors which completely ruled out the effect of the size of the parent stock. Thus, in at least twelve of the nineteen years during the period 1947–1965, the size of the parent stock has apparently not been the primary factor controlling subsequent year-class strength. In the years when numerous year-classes were produced as in 1950 and 1959 other factors (as for instance a more widespread distribution of the spawning grounds and a longer duration of spawning) may have given rise to favourable conditions for the progeny.

In the years 1948–1959 the main spawning took place gradually farther north (DEVOLD 1963) and in 1959–1965 the most important spawning centre was concentrated within area 07 between Stad and Grip. The main spawning grounds within area 06 were located off Halten–Sklinna, and no change in location could be recorded in this area during the period of investigation. In the 1950s spawning off Halten–Sklinna was observed by WIBORG (1954, 1956) and YUDANOV (1962). The locations of spawning off Møre–Trøndelag given by YUDANOV for the period 1959–1965 agree fairly well with the results of the present investigation. Spawning in the area 05 took place mainly during the period 1963–1965. YUDANOV (1962, 1964, 1966) found insignificant spawning in the Lofoten region in 1959, 1961 and 1962, whereas in 1960 a major spawning was found on the banks between Lofoten and Andenes. Spawning in this region has also occurred in previous years as pointed out by RUNNSTRØM (1934), AWERINZEW (1935), RASS (1939) and MARTI (1956).

In the 1930s spawning was found at certain places along the entire coast from Lindesnes to Vesterålen (RUNNSTRØM 1934, 1941a), i.e. off the southwest coast between Lindesnes and Bergen, off the Møre coast and on the banks off Lofoten. The most important spawning region during this period, however, was located within area 08 off the southwestern coast of Norway. Thus, a general restriction of the spawning area has taken place during the 1950s and 1960s, especially in the southernmost spawning region (within area 08) at the same time as the main spawning centre moved farther north. The probability is that the spawning area is more extensive when the spawning stock is large than when the stock size is small. Also the age structure of the spawning stock may have an effect on the extension of the spawning area. However, the change and restriction in spawning area found in 1959–1962 could not only be attributed to the decrease in the size of the spawning stock but also to a real shift in the spawning migration.

DEVOLD (1963) demonstrated that the stock arrived at the coast in area 07 increasingly farther north during the period 1950–1962. During the early 1950s a major part of the stock migrated southward along the coast for spawning, but this did not occur after 1959. The fact that herring shift from one spawning ground to another during their life span is also supported by tagging experiments (DRAGESUND 1961, 1962). Herring tagged on the spawning grounds between Bokn and Stolmen in 1957 and 1958, migrated to the spawning grounds off Møre–Trøndelag the following years. Moreover, the stock component spawning off Lofoten during the period 1963–1966 did not appear on these spawning grounds the following two years, but mixed with the component migrating towards the spawning grounds off Møre–Trøndelag (DEVOLD 1968, JAKOBSSON 1968). This change in location of maximum spawning may have resulted in a simultaneous change in the time of spawning.

To investigate the relationship between the duration of the main spawning period and subsequent year-class strength, the spawning rate has been plotted against year-class strength at six years (Fig. 26A) and at six months (Fig. 26B). The diagrams suggest that high spawning rates resulted in poor year-classes, whereas in years when the main spawning was prolonged stronger year-classes were produced. However, this did not fit in for all year-classes, e.g. those of 1951 and 1953–1955. Long spawning periods often result in prolonged hatching, and it is possible that a larger number of larvae can find suitable and abundant food when they are hatched over a long period than when hatching is restricted in time.

Within the period 1950–1965 the time of main spawning varied (Fig. 5), but no special trend in variation was found. However, in general the main spawning occurred later than it had previously in this century (AASEN 1962, DEVOLD 1963). Between 1904 and 1920 the adult herring arrived at the coast already in October to December, and the main spawning, which took place within area 08, probably commenced earlier than at present time. During the period from 1929 to 1959 the spawning time changed markedly in the spawning region within area 08 (Fig. 27). From 1929 to 1932 the main spawning took place at the beginning of February, and from 1933 to 1939 it occurred in the second half of February. The main spawning time for the period 1929–1939 has been derived from data of RASMUSSEN (1940) by adding ten days to the onset of spawning given in his paper. During the 1950–1959 period the spawning in area 08 occurred during the first half of March. In area 07 (i.e. between Kinn and Grip) no marked change could be found, although the spawning in 1961–1963 took place somewhat later than in the previous years.

During the last three decades the main spawning time thus changed simultaneously with a progressively northward displacement of the main spawning centre. The change in location of maximum spawning and the variations described in spawning time may have resulted in variations in the environmental conditions for the larvae during the period just after hatching. The most striking change is the absence of spawning on the southernmost grounds, between Bokn and Stad, since 1959. In the 1930s and 1940s when the main spawning took place in this region, rich year-classes occurred more frequently (MARTI and FEDOROV 1963, DEVOLD 1963). On the other hand, in the period 1904–1920 when spawning also

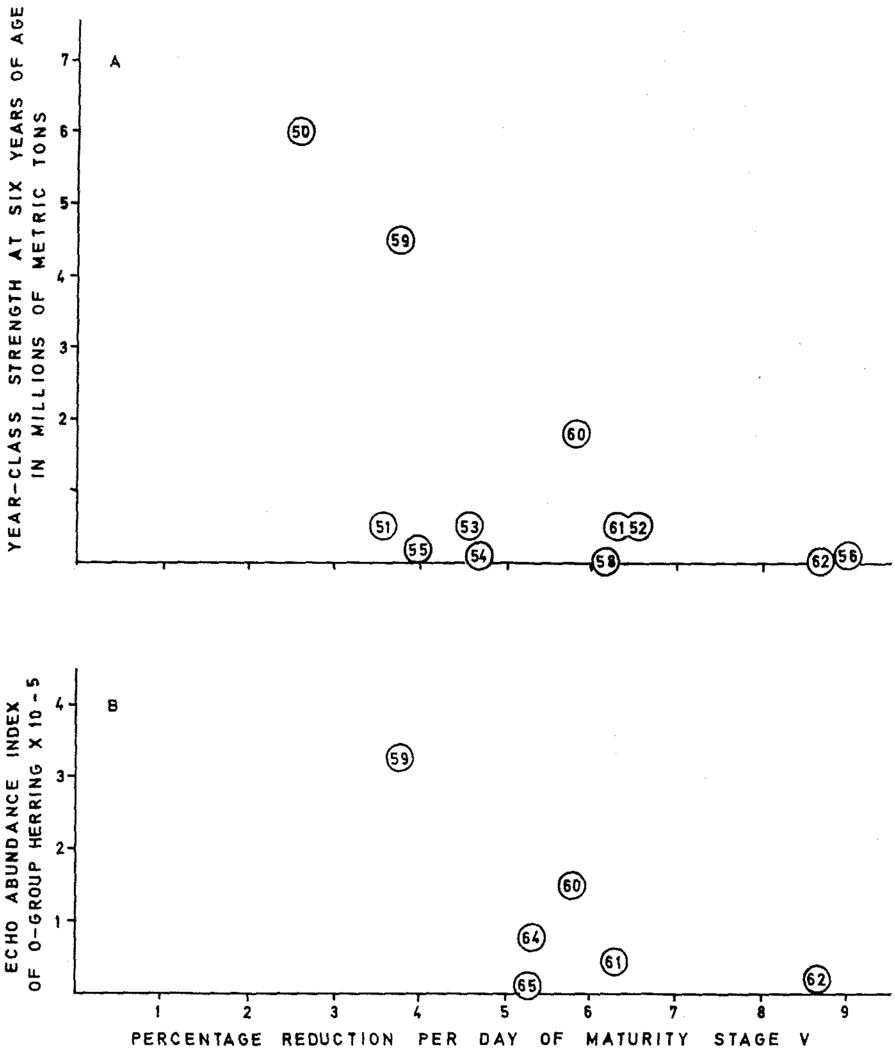

Fig. 26. Relationship between the spawning rate (percentage reduction per day of maturity stage V) within areas 08 and 07 during the spawning seasons in 1950–1965 and subsequent year-class strength, (A) at six years of age for the 1950–1962 year-classes and (B) at about six months of age for the 1959–1965 year-classes. The 1957 and 1963 year-classes are omitted due to insufficient data. The respective year-classes are indicated inside each circle.

took place in the same region, only two rich year-classes were spawned, those of 1904 and 1918. However, during this period the spawning most likely occurred somewhat earlier than in the 1930s (Runnstrøm 1934, Devold 1963), and this feature may have accounted for the long intervals between the appearance of rich year-classes.

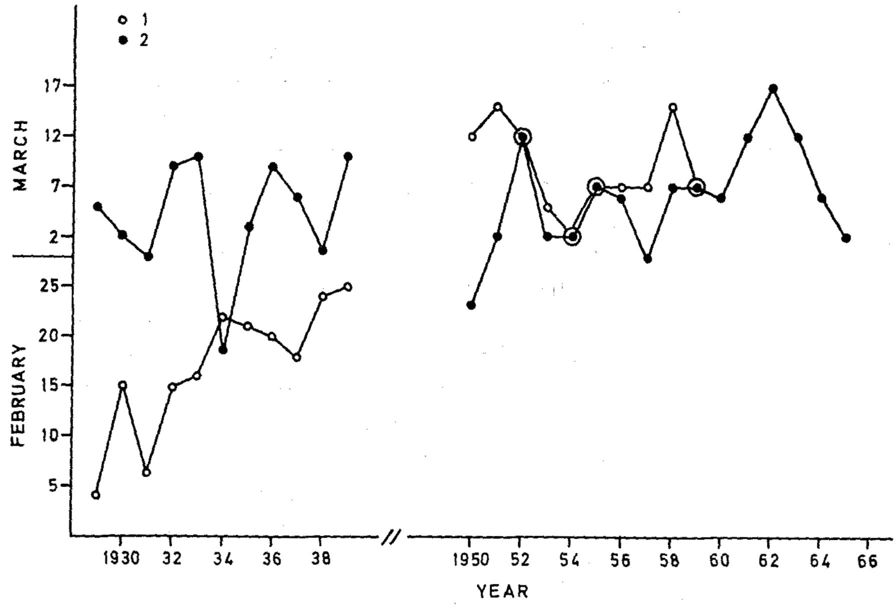

Fig. 27. Time of main spawning during the periods 1929–1939 and 1950–1965, (1) within area 08 and (2) within area 07.

ENVIRONMENTAL CONDITIONS DURING THE EGG STAGE AND EARLY LARVAL DEVELOPMENT

Considerations of environmental factors and their effects on developing eggs and larvae have mainly been concerned with the temperature and thickness of the egg layers. More recently, attention has also been drawn to other factors, as for instance predator effect, pollution and mechanical forces.

Postuma (1968) showed a relationship between the temperature on the spawning bed and year-class strength for Downs and Bank autumn spawning herring and suggested that optimum conditions existed at around 12°C. In the 1930s, when the main spawning of Norwegian herring took place in the southern spawning region (area 08), the most frequent bottom temperature during the spawning season was between 5 and 6°C (Runnstrøm 1941b). During the period 1959–1965, when maximum spawning took place farther north, the temperature varied between 5.5 and 7.5°C on the spawning grounds between Møre and Lofoten. The temperature on the main spawning grounds during the incubation period did not vary markedly from one year to another and cannot be associated with the year-class strength variations during the period 1959–1965.

Lea (1930) showed that thick egg layers on the Norwegian spawning grounds resulted in a high mortality since eggs in the deepest layers were subjected to oxygen deficiency. RUNNSTRØM (1941b) did not find a distinct increase in mortality with increasing density of eggs, except in extremely thick egg layers (10,000 to 12,500 cm^3 per m^2 of sea bed), and the average mortality for the total egg material collected was 12.1%. In the Firth of Clyde, PARRISH *et al.* (1959) showed that only very few dead and unfertilized eggs occurred in the samples, but the stage of development varied through the egg layer. Recent investigations in same area by BAXTER (1968) showed average figures of 3–6% for dead eggs, and there was little indication of higher mortality in the lower layers. For North Sea herring mortality rates of 0–11% (average 4%) were found by HEMPEL and HEMPEL (1968). DRAGESUND and NAKKEN (unpublished) also observed few dead and unfertilized eggs on a spawning site near Grip in 1968. None of these results include mortality at the hatching stage, and mortality during the egg stage seems to be relatively low.

However, gadoid fish feeding on herring eggs have frequently been recorded on the spawning grounds both in the North Sea and along the Norwegian coast. Nothing is known about the frequency of stomach fillings per fish during the spawning season or of the number of fish feeding on herring spawn. The stomach of an adult haddock normally can contain at least the annual egg production of one herring per filling (HEMPEL and HEMPEL 1968, DRAGESUND and NAKKEN unpublished). Therefore, the predator effect may be of some importance.

A second phase of mortality occurs during the hatching period. Experiments carried out on Pacific herring (GALKINA 1968, TAYLOR 1968) indicated that in dense concentrations of eggs the hatching success is rather low. The experiments by TAYLOR showed that the production of viable larvae per unit area often was lower when eggs were packed in eight than when only in four layers. It is not known if these results are applicable for larger stocks of herring reproducing in the open sea. However, LEA (1930) believed that conditions were more favourable for hatching when small quantities of eggs were distributed over a large area than when the spawning was concentrated in a limited region. The present material cannot be used for an analysis of egg concentration in relation to year-class strength. However, heavy packing of eggs is most likely to occur when a large stock spawns during a short period in a restricted area. During the period 1959–1965 the spawning within areas 08, 07 and 06 was more extensive and prolonged in 1959 than in 1962 (Table 14).

The hypothesis of critical periods during early larval development expounded by HJORT (1914, 1926) has been discussed by several authors (e.g. MARR 1956, WIBORG 1957, FARRIS 1960, BEVERTON 1962, GULLAND 1964, HEMPEL 1965). MARR concluded that although catastrophical mortality rates will always remain as a possibility, evidence points towards survival at a constant rate or at a constantly increasing rate, rather than towards the existence of critical periods. GULLAND suggested that mortality is very high just after hatching, and that this is common to all year-classes. Then there is a density-dependent phase in which mortality is higher for year-classes with an initially high number of eggs than for one with an initially low number of eggs. According to GULLAND there is then a phase during which the strength of a year-class is determined, i.e. the phase during which the mortality of an ultimately poor year-class is higher than that of an ultimately rich year-class. Investigations by SOLEIM (1942) indicated a heavy mortality of larvae when the yolk was resorbed. DRAGESUND and NAKKEN (1968) estimated a larval mortality of 94% between a size of 10 mm and a size of 12 mm in 1967. It is likely that such a high mortality at this stage affected the abundance of 0-group herring observed in autumn of 1967 (ANON. 1967). However, comparable larval mortality data for other years are not available. Therefore, it is not possible to estimate the influence of early larval mortality on variations in year-class strength.

The extremes among the year-classes of Norwegian herring spawned during the period 1959–1965 were the rich one of 1959 and the poor ones of 1962 and 1965. Investigations carried out during the 0-group stage (DRAGESUND 1970) showed a considerably higher abundance of the 1959 year-class than of those produced in 1962 and 1965. These results suggest that the mortality of the progeny during the first six months of life may have been considerably higher for the two latter year-classes than for that of 1959. Indication was found that the variation in the size of the spawning stock was reflected in the larval abundance estimates just after hatching (Fig. 19A) and it is, therefore, unlikely that any marked difference in mortality existed before hatching of these year-classes.

When the larvae have resorbed their yolk sacs, suitable food must be available if mass mortality is not to occur. Larvae with poor swimming performance and small field of vision can only search a small volume of water (ROSENTHAL and HEMPEL 1968). For larvae with better vision and better swimming performance, which again is a function of the length of larvae, the volume of water searched every day is far greater. This factor may cause serious competition among larvae during a period of low abundance of food. ROSENTHAL and HEMPEL concluded that the very young larvae are more endangered by malnutrition than somewhat older and larger larvae because they require a higher abundance of food. This feature is in line with the hypothesis of a critical phase of starvation after the yolk stage, and supports the assumption that a restricted and concentrated distribution of larvae just after hatching is disadvantageous.

Advantageous conditions for a high survival of larvae, therefore, should exist when the larvae are dispersed in areas of abundant food supply.

According to BJØRKE (1968) eggs of *Calanus finmarchicus* constituted 93% of the number of particles in the gut content of larvae investigated in 1967 off Møre during a three-week period from the time of hatching. LIE (1965) found that spawning of *Calanus finmarchicus* at Sognesjøen started in the first half of March in 1959, whereas the spawning in 1962 started later, probably in early April. Thus, the spawning of *Calanus* occurred earlier in relation to the hatching of herring larvae in 1959 than in 1962 (Fig. 28). The spring spawning of *Calanus* is followed by an increase in the zooplankton biomass. In 1962 the mean total volume of zooplankton at Sognesjøen in April and May was considerably lower than in 1959, indicating less available food for herring in 1962. On the other hand, no such differences either in time of spawning or in total plankton volume were found between the two seasons at the Skrova and Eggum stations in the Lofoten region (LIE 1965). However, these stations are located farther north of the areas where the main concentrations of herring larvae at yolk resorption were observed than Sognesjøen is located south of these areas. In 1965 the spawning of *Calanus* took place in February–March at the Sognesjøen station (LIE 1966) and the hatching of herring larvae off Møre occurred during the second half of March (Fig. 28). The hatching of herring larvae off Lofoten occurred relatively early in 1965 (about 20 March). The spawning of *Calanus* took place in March–April (LIE 1966) and it is possible that the coincidence in time between the *Calanus* spawning and hatching of herring larvae in 1965 may have been unfavourable.

The importance of abiotic factors, as for instance wind direction and force influencing year-class strength, have been stressed by several authors (SETTE 1943, CARRUTHERS *et al.* 1951, HILL and LEE 1957, BAKKEN 1966). HILL and LEE suggested that there was a positive correlation between rich year-classes of Arctic-Norwegian cod and strong southerly wind during the period when the larvae drift from the Lofoten spawning grounds to the Bear Island area. A similar relationship was found for herring larvae. The northward drift of larvae is hampered in years with relatively weak winds or prevailing westerly and northerly winds. This feature has probably added to the effect of a concentrated spawning in 1961 and 1962, resulting in a relatively restricted distribution. In 1961 a rather rapid northward drift took place on the southern spawning grounds just after hatching, whereas farther north the wind had a diminishing effect on the northward larval drift and led to a concentrated distribution. In 1959, 1960, 1963 and 1964, spawning took place over a wider area and the prevailing southerly winds during and just after hatching resulted in a

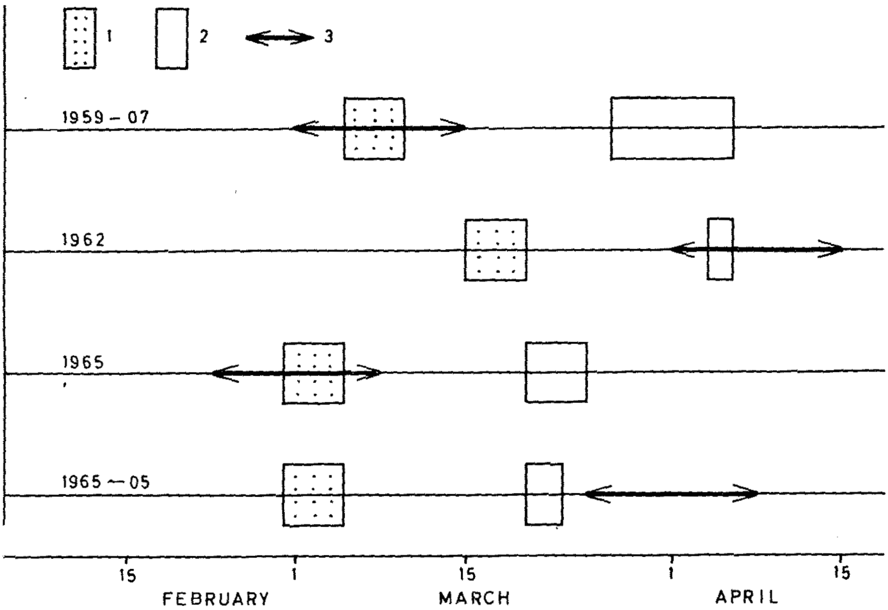

Fig. 28. Time of, (1) main spawning and (2) main hatching of herring compared with (3) time of the first spawning of *Calanus finmarchicus* at Sognesjøen (area 07) and off Eggum (area 05) in 1959, 1962 and 1965.

rapid dispersion of larvae from the spawning grounds. Also, the long duration of the spawning in these years added to the effect of southerly winds and resulted in a dispersed distribution.

Benko and Seliverstov (1968) and Postuma (1968) concluded that the water temperature during the larval and postlarval periods is an important factor controlling the success or failure of recruitment. Benko and Seliverstov found a positive correlation between the surface temperature during the larval stage and the year-class strength of Norwegian herring for the period 1948–1965. The underlying mechanism of the effects of temperature on larval mortality is complex. Temperature affects metabolic rate, i.e. incubation time, rate of growth, rate of resorption of the body reserves, swimming speed, food demand, etc. (Beverton and Holt 1957, Hempel 1965). It also affects the abundance and species composition of food plankton and predators. If the larvae are distributed in water with a relatively high temperature immediately following hatching, they may pass rapidly through critical stages. Nakken (1966) has shown a positive correlation between high temperatures in the coastal water and the current velocity. The relatively high temperatures found off Ona, Sula (near Nordøyane) and Myken (near Træna) in March and April 1959 and 1960 and partly in 1961, 1963 and 1965 (Benko and

Table 14. Summary of factors considered to be of importance in determining year-class strength of Norwegian herring compared with abundance estimates obtained at the 0-group stage and at six years of age for the 1959–1965 year-classes.

Factor	Area	Spawning year						
		1959	1960	1961	1962	1963	1964	1965
Spawning stock size in mill. tons (Fig. 2)	07 06	5.5	4.5?	3.5?	2.5	2.9	4.2	7.3
Mean age of spawning stock (Table 6)	07	9.5	10.3	10.7	11.7	12.2	8.7	7.8
	06	9.5	—	—	11.7	11.6	—	5.4
	05	—	—	—	—	3.9	4.9	5.7
Extension of spawning area, indicated by number of rectangles, where herring in spawning and spent condition were caught (Table 8)	08	2	0	0	0	0	0	0
	07	8	8	6	4	5	5	5
	06	9	9?	5?	7	6	7	9
	05	?	?	?	?	5	5	6
Approximate northward displacement (in nautical miles) of spawning centres, reference year 1959 (Fig. 3)	07	Centre: Off Stad	30	60	60	70	90	90
	06	Halten-Sklinna	0	0	0	0	0	0
Duration of spawning season in days (Fig. 4)	07	30	30	30	20	20	20	20
	05	—	—	—	—	10	10	20
Date of main spawning (Fig. 4)	07	5–9.3	5–9.3	10–14.3	15–19.3	10–14.3	5–9.3	28.2–4.3
	05	—	—	—	—	25–29.3	25–29.3	28.2–4.3
Spawning rate (Table 10)	07	3.8	5.9	6.3	8.7	?	5.3	5.3
	05	—	—	—	—	?	22.0	10.3
Date of main hatching (Fig. 7)	07	26.3–5.4	23–31.3	29.3–3.4	4–6.4	30.3–11.4	25–26.3	20–25.3
	05	—	—	—	—	16–26.4	15–19.4	20–23.3

Direction and relative strength of the mean wind vectors for March–April (Fig. 21)	07	20°	34°	62°	29°	325°	342°	45°
		120	60	180	50	85	55	90
	06	357°	354°	88°	91°	334°	50°	35°
		160	190	160	50	180	100	75
	05	20°	12°	135°	160°	310°	326°	5°
		130	200	130	80	75	60	20
First spawning period of *Calanus finmarchicus* (LIE 1965, 1966)	Sognesjøen	1–15.3	1–15.3	1–15.3	1–15.4	Feb.–March	Feb.–March	Feb.–March
	Eggum	—	1–15.4	1–15.4	1–15.4	April	April	April
Year-class strength at six months of age, echo abundance index $\times 10^{-3}$ (DRAGESUND 1970)		325.8	147.4	37.5	14.8	53.6	75.0	9.1
Year-class strength at six years of age (in mill. tons)		4.5	1.8	0.5	0.03	—	—	—

SELIVERSTOV 1968) also may have been associated with higher velocity of the coastal current those years than in 1962 and 1965 when lower temperatures were found at these stations.

Table 14 compiles information from preceding chapters on factors to be of importance in determining year-class strength of herring during the period 1959–1965. The data indicate that within the range of observed stock size a relationship might exist between the parent stock and abundance of the resulting year-classes when favourable conditions occurred. However, in most of the years during the period 1947–1965, year-class strength was determined by a complex of other factors which completely ruled out the effect of the parent stock size. The following factors are considered to be most important in determining year-class strength:

1) the extent of the spawning area;
2) the duration of the main spawning season;
3) the rate of dispersion of larvae from the spawning grounds;
4) the coincidence in time between the availability of suitable food and hatching of herring larvae.

In 1959, 1960, 1963 and 1964, spawning was extensive and prolonged with a rapid dispersion of larvae from the different spawning grounds. The opposite conditions existed in 1962. In 1965 spawning was extensive and in 1961 relatively prolonged, but the conditions for transport of the larvae during the period after hatching resulted in a concentrated distribution. The gradual northward displacement of the main spawning centre during the last two decades probably has increased the importance of the timing factor, since only two definitely numerous year-classes occurred during the period 1950–1965, namely those of 1950 and 1959.

SUMMARY

1. Variation in year-class strength of Norwegian spring spawning herring is analysed in relation to the structure and the size of the spawning stock, the location and the time of spawning and environmental conditions during the egg stage and the early larval development with special reference to the 1959–1965 year-classes.

2. Stock size estimates were obtained from tagging experiments, and the number of eggs spawned in each year was calculated from fecundity data in the literature. The highest figure for the stock size (7.3 million tons) was found in 1965. The stock size had its lowest figure in 1962 when it was about 2.5 million tons.

3. The location of spawning was determined from the distribution of catches of spawning and spent herring and from the distribution of newly

hatched larvae. During the period 1959–1965 the most important spawning took place off Møre, i.e. on the shelf between Stad and Grip, and mainly in depths of less than 200 m. Spawning south of Bergen was negligible except in 1959. During the entire period spawning took place off Halten and Sklinna, whereas spawning at Lofoten was more sporadic.

4. The duration of the spawning season was determined from the maturity composition of herring collected several times a week during the spawning season. Off Møre spawning was late in 1962 (15–19 March) and early in 1965 (28 February–4 March). In 1963 spawning off Lofoten occurred about two weeks later than off Møre, and in 1964 three weeks later, whereas in 1965 spawning took place about simultaneously in the two regions.

5. The time of main hatching was estimated by adding an incubation period of generally 18–24 days (depending on the temperature) to the time of main spawning. Approximate figures for the incubation periods were obtained from the literature.

6. The distribution of herring larvae during the first month after hatching was analysed for the period 1959–1965. The larvae were collected with Clarke-Bumpus plankton samplers in oblique hauls during regular surveys covering the coastal banks between Stad and Lofoten. Factors affecting larval abundance estimates are discussed, and a general description of the vertical distribution and diurnal migration of herring larvae is given. The geographical distribution of larvae was analysed in relation to the spawning grounds. The drift of larvae was inferred from subsurface drogue experiments, wind observations and drift bottle experiments. Larval length was analysed in relation to the time of spawning. During the first month after hatching the larvae were concentrated near the coast, and almost no larvae were found outside the edge of the shelf. A more concentrated distribution of larvae was observed in 1961, 1962 and 1965 than in the other years considered. The larvae are transported northward in coastal water and the force and direction of the wind play an important role in determining the distribution pattern of larvae.

7. The results indicated that within the range of observed stock sizes a relationship may exist between the parent stock and abundance of the resulting year-classes when favourable conditions occurred. However, it is likely that the year-class strength was determined by a complex of other factors which completely ruled out the effect of parent stock size in most of the years. Conditions assumed to be advantageous for the development of strong year-classes were inferred from the present and other investigations. Strong year-classes seemed to occur when a combination of the following conditions existed:

1) widespread distribution of spawning;
2) long duration of the spawning period;
3) a rapid dispersion of larvae from the spawning grounds.

In 1959, 1960, 1963 and 1964, spawning was extensive and prolonged and with a rapid northward dispersion of larvae from the different spawning grounds. In 1962 the opposite conditions existed. Spawning was extensive in 1965 and prolonged in 1961, but the transport conditions during and after the yolk sac stage resulted in a concentrated distribution pattern.

8. The coincidence in time between the occurrence of suitable food and hatching of herring larvae is assumed to be the most important environmental factor controlling year-class strength during the early larval development. The gradual northward displacement of the main spawning centre during the last decades probably has increased the importance of the timing factor, since only two definitely rich year-classes occurred during the period 1947–1965, namely those of 1950 and 1959.

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TABLES

Table I. Number of larvae below 1 m² of surface caught with Clarke–Bumpus plankton samplers in two subsequent pairs of oblique hauls off Halten in 1964.

Date	Series 1				Series 2			
	Hour	25–5 m	50–30 m	Total	Hour	25–5 m	50–30 m	Total
16.4	1730	5	0	5	1800	0	0	0
	1937	2	0	2	2005	0	0	0
16–17.4	2350	37	16	53	0020	45	30	75
17.4	0152	18	11	29	0225	27	7	34
	0400	9	4	13	0428	2	2	4
	0605	4	0	4	0730	10	0	10
	0840	3	2	5	0910	3	2	5
	1503	0	4	4	1530	2	2	4

Table II. Number of larvae below 1 m² of surface caught in oblique hauls with pairs of Clarke–Bumpus plankton samplers attached 1 m apart, off Eggum (23–29 April) and off Træna (30 April–1 May) in 1964.

Date	Series 1			Series 2		
	Hour	24–4 m	25–5 m	Hour	49–29 m	50–30 m
23.4	0115	162	290	0320	338	280
	—	—	—	0505	348	263
28.4	1105	27	50	1315	135	161
	1455	43	47	1715	67	42
	1900	69	70	2110	43	23
28–29.4	2310	69	120	0110	106	49
29.4	0310	76	64	0508	132	58
	0705	87	85	0910	134	82
30.4–1.5	2345	31	29	0105	12	11
1.5	0300	2	10	0524	0	0
	0741	10	23	0940	2	0

Table III. Number of larvae below 1 m² of surface caught in oblique hauls with Clarke–Bumpus plankton samplers close to subsurface drogues at drift station 2 off Sklinna (18–19 April, 1964), at drift station 4 off Eggum (28–29 April, 1964) and at drift station 5 off Frøya (9–10 April, 1965).

Date		Hour	25–5 m	50–30 m	75–55 m	Total
1964	18.4	1340	5	5		10
		1600	0	0		0
		1820	9	13		22
		2005	6	12		18
		2205	64	7		71
	19.4	0015	39	2		41
		0213	49	16		65
		0420	29	9		38
		0605	6	12		18
		0805	13	6		19
		1000	2	2		4
		1205	9	4		13
		1400	2	4		6
1964	28.4	0920	74	91		165
		1105	50	117		167
		1315	66	161		227
		1455	47	58		105
		1715	52	42		94
		1920	70	45		115
		2110	94	23		117
		2310	120	60		180
	29.4	0110	199	49		248
		0310	64	53		117
		0508	120	58		178
		0705	85	108		193
		0910	53	82		135
1965	9.4	1415	18	34	21	73
		1617	21	71	24	116
		1829	9	94	42	145
		2020	115	43	16	174
		2220	53	77	7	137
	10.4	0035	18	18	0	36
		0210	121	29	2	152
		0414	60	18	3	81
		0624	15	69	0	84
		0820	0	23	2	25
		1015	0	17	4	21
		1120	0	30	7	37

Table IV. Composition (in %) of the maturity stages of Norwegian herring in five-day periods during the spawning seasons in 1959–1965.

Area		Date	No.	Maturity stage			
				IV	V	VI	VII
08	1959	23–27.2	177	4.0	48.6	36.1	11.3
		28.2–4.3	89	—	9.0	85.4	5.6
		5–9.3	272	—	9.9	83.5	6.6
		10–14.3	188	—	2.1	74.5	23.4
		15–19.3	90	—	—	90.0	10.0
07	1959	8–12.2	640	8.6	89.4	2.0	—
		13–17.2	217	2.3	96.3	1.4	—
		23–27.2	264	0.8	43.8	27.7	27.7
		28.2–4.3	364	0.3	16.2	28.3	55.2
		5–9.3	90	—	15.6	32.2	52.2
		10–14.3	186	—	7.0	73.1	19.9
08 and 07	1959	8–12.2	640	8.6	89.4	2.0	—
		13–17.2	217	2.3	96.3	1.4	—
		23–27.2	441	2.0	45.8	31.1	21.1
		28.2–4.3	453	0.2	14.8	39.5	45.5
		5–9.3	362	—	11.3	70.7	18.0
		10–14.3	374	—	4.5	73.8	21.7
		15–19.3	90	—	—	90.0	10.0
07	1960	13–17.2	1182	4.8	94.9	0.3	—
		18–22.2	1039	2.1	96.9	0.9	0.1
		23–27.2	703	—	65.7	30.9	3.4
		28.2–3.3	280	—	7.9	86.8	5.3
		4–8.3	345	—	16.2	62.3	21.5
		9–13.3	308	—	0.7	96.1	3.2
		14–18.3	134	—	3.7	88.1	8.2
07	1961	13–17.2	404	18.6	78.5	2.7	0.2
		18–22.2	531	5.3	91.9	2.8	—
		23–27.2	704	4.7	83.8	9.2	2.3
		28.2–4.3	516	0.2	33.0	30.8	36.0
		5–9.3	227	—	2.7	75.3	22.0
		10–14.3	182	—	1.1	72.5	26.4
		15–19.3	46	—	4.3	45.7	50.0
07	1962	28.2–4.3	1052	5.3	94.2	0.5	—
		5–9.3	888	0.8	82.3	11.3	5.6
		10–14.3	662	—	8.0	39.6	52.4
		15–19.3	128	—	1.6	18.0	80.4
		20–24.3	112	—	0.9	4.5	94.6

Table IV (*continued*)

Area	Date		No.	Maturity stage			
				IV	V	VI	VII
07	1963	28.2–4.3	430	3.3	66.7	29.3	0.7
		5–9.3	214	2.8	7.0	71.5	18.7
		10–14.3	116	—	—	85.3	14.7
		15–19.3	974	—	0.4	65.5	34.1
		20–24.3	204	—	—	32.8	67.2
05	1963	20–24.3	77	37.7	—	9.1	53.2
		25–29.3	264	5.3	7.2	85.2	2.3
		30.3–3.4	93	—	—	—	100.0
07	1964	13–17.2	365	18.4	81.3	0.3	—
		18–22.2	461	4.8	91.3	3.9	—
		23–27.2	636	0.6	59.0	39.6	0.8
		28.2–3.3	320	0.6	22.5	53.1	23.8
		4–8.3	315	—	8.9	67.0	24.1
05	1964	28.2–3.3	82	2.4	97.6	—	—
		4–8.3	94	—	—	100.0	—
		9–13.3	95	—	2.1	97.9	—
		14–18.3	540	—	0.2	99.8	—
		19–23.3	365	—	—	99.2	0.8
07	1965	13–17.2	317	11.4	88.6	—	—
		18–22.2	404	3.5	77.2	19.1	0.2
		23–27.2	248	0.4	29.9	66.1	3.6
		28.2–4.3	205	1.0	3.4	75.1	20.5
		5–9.3	96	—	1.0	93.8	5.2
05	1965	13–17.2	95	2.1	92.6	5.3	—
		18–22.2	175	4.6	83.4	11.4	0.6
		23–27.2	94	—	2.1	95.8	2.1
		28.2–4.3	187	—	1.6	57.8	40.6
		5–9.3	92	1.1	10.9	46.7	41.3