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A method to estimate the annual larval production of the Norwegian spring- spawning Herring (*Clupea harengus* L.)

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A comprehensive survey in the larval distribution area of Norwegian spring-spawning herring along the Norwegian west coast was carried out annually by the Institute of Marine Research, Bergen in the years 1986-1990. Moreover, two small subareas were sampled repeatedly (usually twice a week) off Sunnmøre and at Buagrunnen throughout the hatching period each year. The daily larval production was worked out with the data obtained from the comprehensive survey covering the entire larval distribution area. Data obtained in the subareas had been used to construction the hatching curve so as to get the daily larval production percentage in the hatching period. Then, the annual larval productions were estimated. The annual larval production from 1986 to 1990 were 1.7×10^{12}, 3.9×10^{12}, 35.4×10^{12}, 72.8×10^{12} and 99.1×10^{12} individuals.

Key words: hatching, larva production, the Norwegian spring-spawning herring

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Introduction

Field investigation of the eggs and larvae of marine fin fish originated in the late 1800s. The motivations for investigations have changed little up to now, which is mainly the assessment of adult spawning biomass and the distribution of eggs and larvae, and the desire to understand how environmental variations and changes in the abundance of other species interact in order to regulate the abundance of a stock (Heath, 1992).

Annual surveys of larval herring for estimating spawning stock size have been widely used in the North Atlantic. In the southern North Sea surveys began in 1946 (Bridger, 1960, 1961) and in 1951 in the northern North Sea (Saville, 1971), and have continued ever since. Cushing and Bridger (1966) first demonstrated a relationship between larval abundance and spawning stock biomass, and since 1967 the co-ordination of surveys by several European nations has been organised under the auspices of the International Council for the Exploration of the Sea (ICES). Off the east coast of USA and Canada (Georges Bank - Bay of Fundy) annual larval abundance surveys since 1972 have been co-ordinated through the International Commission for Northwest Atlantic Fisheries (ICNAF).

Norwegian spring-spawning herring (*Clupea harengus* L.) is the largest stock of the Atlanto-Scandian herring tribe. The spawning takes place during February to April and the spawning grounds are situated mainly along the Norwegian west coast (Runnstrøm, 1941; Dragesund, Hamre and Ulltang, 1980; Bakken, 1983).

The methods to estimate the larval production are of acoustics and biology. The biological method needs much information of the developmental biology and ecology, it is a direct method.

Material and Methods

The collections of the herring larvae were conducted mainly in the area $61^0$30'N - $66^0$00'N close to the Norwegian west coast during March and April each year from 1986 to 1990. Sampling was carried out in

two steps: i) surveying the entire larval distributional area with an ocean-going research vessel twice during a hatching season. In 1990, however, only one cruise was arranged. ii) repeated sampling a set of fixed stations off Sunnmøre and at Buagrunnen separately throughout the hatching period.

The herring larvae were sampled with a modified conical net (T 80) with a 0.5 m^2 opening and 375 μm mesh size (Ellertsen, Fossum, Solemdal, Sundby and Tilseth, 1984). The vertical hauls were taken from 150 m depth (or 5 m above bottom) to the surface with a hauling speed of 0.5 ms^{-1} (Fossum, 1990). The larvae were sorted and counted from the sampling buckets, and up to 50 (or those caught if less than 50) were measured for standard length (SL). The measurements were taken on board to the nearest mm below. The larvae were preserved in 2% or 4% formalin. In the laboratory, 20 larvae (or those caught if less than 20) from each station were staged according to the scale given by Doyle (1977). Some larvae were also staged fresh on board (Fossum *et al.*, 1987; Sure *et al.*, 1988 and Fossum, 1990).

The mean duration of the different substages during the surveyed years were set out by Fossum (1990) after studying several scientists' work (Table 1). The standard lengths (SL) of larvae in each substage are only available for the 1986 data (Fossum *et al.*, 1987) (Table 1).

Table 1. Mean duration of yolk-sac larval stages 1a, 1b, and 1c and mean standard length in each stage for the larvae of the Norwegian spring-spawning herring

Stage	1a	1b	1c
Duration (d)	3	4	3
Length (mm)	8.1 (0.8)	9.1 (0.9)	10.0 (0.8)

*standard deviations for the length measurement are given in parenthesis.

The number of larvae per m^2 surface (N) was calculated by the formula:

$$N = \frac{n \times d}{v} = \frac{n \times d}{a \times d} = \frac{n}{a} \qquad (1)$$

where n is the number of larvae in a sample; d is the depth interval; v is the water volume filtered through the net; a is the opening area of the net, here is 0.5 m^2.

The one-day cruises sampling the 7 fixed stations off Sunnmøre (from $62^0$00'N to $63^0$00'N) and the 5 at Buagrunnen (from $63^0$00'N to $64^0$00'N) were carried out separately. These surveys were aimed at covering the whole of the hatching season, i.e. to start before the first eggs hatched and to stop after all eggs had hatched. They were repeated twice a week throughout a hatching season. All the stations were selected on the basis of previous knowledge of the location of spawning grounds.

The sampling net and operation were the same as applied in the survey of the entire larval distributional area. The number of larvae per m^2 surface were calculated applying equation (1).

If bad weather prevented any station from being sampled during the cruises, attempts were made to take a sample at a location, as close as possible to the original station (Bjørke and Rey, 1991).

Construction of the hatching curve

The hatching curves were plotted with the percentage of daily larval production versus the corresponding date. One curve was constructed with the data collected at the fixed stations off Sunnmøre, another with the data collected at the fixed stations at Buagrunnen.

In the calculations, a 1 m^2 surface was taken as the standard unit area. To obtain the average daily larval production per m^2 surface, at first, the number of 1b larvae sampled at each station was converted into the number per m^2 surface applying equation (1). Then, the average number of 1b larvae per m^2 surface at the stations sampled in a one-day cruise was worked out. According to Table 1, the duration of the 1b larval substage is 4 d, the ages of the 1b larvae are from the 4th day to the 7th day, and the average age of 1b larvae is therefore 5 d. Hence, the larval production estimated from the number of 1b larvae sampled in one day is the cumulative larval production during 4 d. It is given as follows:

$$N_0 = N_t \times e^{(M \times t)} \qquad (2)$$

where N_0 is the cumulative larval production during 4 d; N_t is the number of 1b larvae sampled in one day; M is the daily larval mortality (a value of 0.1 per day was used (Christensen, 1985)); t is the age of larvae in d, 5 d on average for 1b larvae. Assuming that the daily larval production during the 4 d was constant, it is ¼ of the cumulative larval production. Thus, the average daily larval production per m^2 surface from the 7th to the 4th day before the day when the 1b larvae were sampled, were obtained.

The beginning of the hatching season was indicated by the earliest hatching day of the larvae sampled in the first few cruises, and the end of the hatching season was indicated by the latest hatching day of the larvae sampled in the last few cruises, provided the entire hatching season was covered.

After the average daily larval productions per m^2 surface were worked out, they were converted into their percentage of the total annual larval production per m^2 surface. Assuming that the average daily larval production per m^2 surface is representative of that in the entire larval distributional area, the daily percentage is hence representative of that of the total larval production on the given day.

Considering hatching could be a continuous process, the hatching curves were smoothed using the equation:

$$P_j' = \frac{P_{j-1} + 2P_j + P_{j+1}}{4} \qquad (3)$$

where P_j' is the smoothed percentage of larval production on day j. P_{j-1} P_j and P_{j+1} are the percentages of larval production on day (j-1), j and (j+1) respectively.

The Kolmogorov-Smirnov Two-Sample Test (Sokal and Rohlf, 1981) was then used to test the null hypothesis of no significant difference between the progression of hatching in the two areas. If the hypotheses could not be rejected, one hatching curve was constructed with the pooled data from off Sunnmøre and at Buagrunnen. If the hypothesis could be rejected, one hatching curve was constructed separately for each area. It was assumed that the hatching curve off Sunnmøre represented the hatching pattern not only in the area from $62^0$00'N to $63^0$00'N but also in the surveyed area south of $62^0$00'N, and that the hatching curve at Buagrunnen represented the hatching pattern not only in the area from $63^0$00'N to $64^0$00'N but also in the surveyed area north of $64^0$00'N.

Calculation of daily larval production

The daily larval production was computed using the quantity of 1b larvae (in 1986 the 9.0-9.9 mm SL group) sampled by the ocean-going vessel. The larval abundance during a cruise was calculated with a computer programme made at the Institute of Marine Research, Bergen (Westgård *et al.*, 1988).

This programme integrates larval abundance by dividing the entire larval distributional area into many small rectangles. The assumption for the estimation was that the observation in a rectangle represent not only the point in space at which it was taken but the whole area within the rectangle. If several stations were located in a rectangle, the average larval abundance for these stations was used.

The quantity of lb larvae was used to calculated the number of newly hatched larvae by applying equation (2). As the 1b larvae sampled in a given day is the cumulative larval production during 4 d, the back-calculated number of larvae was divided by 4 to get the average daily larval production during the 4 d.

In 1986, the larvae sampled in the survey were not staged by the development of the yolk-sac. As shown in Table 1, the standard length of 1b larvae was 9.1 mm (SD=0.9). Hence, the abundance of the larvae in the 9.0-9.9 mm group was used to estimate the larval production in this year. According to Fossum (1990), the growth rate of larvae shorter than 10 mm in 1986 was 0.25 mm per day. This means that the larvae needed 4 d to grow through the length of 9.0 - 9.9 mm. Assuming the average hatching length of the larvae was 8 mm (Table 1), the ages of larvae in 9.0 - 9.9 mm group were from 5 d to 8 d, the average age was 6 d. Therefore, the daily larval production can also be obtained following the procedure outlined above.

Estimation of annual larval production

The annual larval production is given by the equation:

$$L = \frac{N_0}{\sum_{j=1}^{n} P_j} \times 100 \qquad (4)$$

where L is the annual larval production; N_0 is the larval production in a hatching period; p_j is as defined in equation (3); n is the number of days in the hatching period.

As mentioned previously, two cruises were usually carried outduring a hatching season. The estimate of seasonal larval production was weighted by the cumulative percentages in the two hatching periods as follows:

$$L = = \frac{N1_0 + N2_0}{\sum_{i=1}^{n} P1_i + \sum_{j=1}^{m} P2_j} \qquad (5)$$

where $N1_0$ and $N2_0$ are the numbers of hatched larvae in hatching period 1 and 2 respectively; $P1_j$ and $P2_j$ are percentages of the daily larval productions in the hatching period 1 and 2 in the annual larval

production, n and m are the number of days in the period 1 and period 2.

Results

Annual larval production

Hatching curves

The length of the hatching season in an area varied between years up to 16 d. The shortest hatching season observed was in 1989 with 36 d, the longest in 1986 with 52 d (Table 2). The null hypothesis of no significant difference between the progression of hatching at the two locations was rejected ($D \times n_1 \times n_2 = 20$, $P<P_{0.1}=24$, $D=0.8$, $n_1=n_2=5$). The seasonal larval production in the two areas was therefore calculated separately.

Table 2. Length of the hatching season off the Sunnmøre and at the Buagrunnen spawning grounds in the years 1986-1990.

	Sunnmøre		Buagrunnen	
Year	Period	No. of d	Period	No. of d
1986	10/3-25/4	47	6/3-26/4	52
1987	5/3-25/4	52	8/3-22/4	46
1988	15/3-29/4	46	14/3-30/3	48
1989	14/3-19/4	37	11/3-15/4	36
1990	9/3-21/4	44	9/3-14/4	37

The two corresponding series of hatching curves are shown in Fig.1. The curves are generally not bell-shaped, but rather poly-modal and in some years highly skewed (e.g. Sunnmøre 1988).

Estimate of annual larval production

The annual larval productions were estimated with information on the progression of hatching shown in Table 2. The estimates gave higher values in 1989 and 1990, lower in 1986, 1987 (Table 3).

Table 3 Total larval production of Norwegian spring-spawning herring in each spawning seasons 1986-1990. The figures given are number x 10^{12}.

Year	1986	1987	1988	1989	1990
Estimate	1.7	3.9	35.4	72.8	99.1

Discussion

Use of the yolk-sac development substage 1b larvae

Seliverstov (1974) studied the larvae of the Atlanto-Scandian herring off the Norwegian west coast. He observed the behaviour of newly hatched larvae in aquaria and found that during the first 12 hours they did not respond to light or had a weak negative phototaxis. Two days after hatching most larvae were able to remain in mid-water and possessed a strong positive phototaxis. In the open sea, therefore, larvae presumably move to pelagic layers during the second day. Comparison of the age composition of larvae collected on the spawning grounds with that of larvae reared under artificial conditions showed that in the sea larvae with an age of about 5 d predominated in the upper 50 - 100 m layer of the water column, i.e. over 3-3.5 d they migrate 50 m upwards if spawning depth is 100-150 m. This experiment should document that 1b larvae are distributed off the bottom and therefore are more available for sampling during the surveys than the larvae in substage 1a.

At the end of substage 1c, the herring larvae have absorbed their yolk-sac completely. In this period, larvae experience a high mortality if there is lack of suitable food (Dragesund and Nakken, 1971; Cushing, 1990). If the number of 1c larvae is used to estimate the spawning stock size, inaccurate estimates of mortality due to higher age would bring bigger error into the assessment of the annual larval production than using the number of 1b larvae. From an overall evaluation, the quantity of larvae in substage 1b was therefore applied to estimate the herring larval production.

One point to be kept in mind is that the duration of substage 1a is affected both by the amount of yolk present at hatching and by temperature, and the duration of substage 1b is affected by temperature (Fossum, 1986). The experiment done by Fossum (1986) shows that the duration of substage 1b is 1.2and 3.3 days at 9^0C and 6^0C respectively. According to the hydrography data collected during the larval surveys (database supplied by the Institute of Marine Research, Bergen), the surface temperature in the entire larval distributional area during the survey periods ranged from 4.5^0C-6.5^0C.

Sampling gear

The sampler used in the present study was the T-80 net. There is a bridle with a triangle attachment mounted in front of it. In this study the net was hauled vertically with a speed of 0.5 ms^{-1}. The catching efficiency of the T-80 net has been compared with the high-speed Gulf III sampler for sampling capelin larvae in the Barents Sea and was found to be low (H. Bjorke, Institute of Marine Research, Bergen, unpublished data). The Gulf III sampler caught from 7 to 49 times more capelin larvae of all length groups than the T-80 sampler. The average length of the sampled larvae was 9.82 mm in the Gulf III sampler and 8.87 mm in the T-80. The catch ratio was generally 9:1 in favour of the Gulf III sampler.

The vital difference between the two sampling devices may be that the Gulf III runs at a high speed and therefore is able to minimize the effect of avoidance to the net of the large larvae. Heath (1992) stated that in general, the low towing speed of the Bongo net and some other framed nets preclude their use for quantitative sampling of active larvae. The high-speed (3 ms^{-1}) Gulf-III type samplers are preferable (Brander and Thompson, 1989). The catching efficiency increases with increasing net speed, and the larger fish larvae avoid nets towed at low speed to a greater extent than do the smaller larvae (Clutter and Anraku, 1968). Hence, for estimation of larval production, it is optimum to use the high speed sampler.

Sampled areas

The area sampled on the first cruise in 1986 was from $62^0$00'N to $63^0$30'N, and did not extend to the south of $62^0$00'N and north of $63^0$30'N where larvae were sampled in the later years. On the second cruise in 1986, only a few stations were located to the north of $64^0$00'N, and no sampling was carried out to the south of $62^0$00'N. In 1988 to 1990, there was high density of larvae in the area from $61^0$30'N to $62^0$00'N, but only a few of the sampled stations were located in this area close to shore. Rottingen (1989) wrote that spawning herring in 1989 were recorded off Karmøy (approximately 59^0N). There has been reports of spawning herring from areas as far south as Siragrunnen (approximately 58^0N). Prior to 1955, this was the important spawning grounds for Norwegian spring-spawning herring. Thus, the coverages of the larval distributional areas should be increased in the further surveys.

Damaged larvae during sampling

During the surveys some yolk-sac larvae were damaged with their yolk-sacs torn away. This made the classification based on the development of the yolk-sac impossible. Thus all the damaged larvae were excluded from the analysis and put in a separate individual group called stage 94. Except for 1987, damaged larvae made up a significant proportion (10-25%) of the yolk-sac larvae (Table 4).

The relative percentage of 1b larvae of the identifiable yolk-sac larvae varied considerably (30-60%) among the years 1987-90 (Table 5). If the relative proportion of damaged larval is the same for all substage (Table 4; Table 5), the number of 1b larvae will in some years be seriously underestimated (e.g. 1988). Consequently the larval productions will also be underestimated. Due to the relatively larger size of the yolk-sac, 1a larvae may be more vulnerable to damage than larvae in other substages.

Table 4. Percentage of the total number of yolk-sac larvae caught that could not be classified due to damage (stage 94).

Year	1987	1988	1989	1990
Percent damaged (%)	1.3	16.3	10.5	24.4

Table 5. Proportion of 1a, 1b, and 1c yolk-sac larvae among the sampled non-damaged larvae.

	Year			
Stage	1987	1988	1989	1990
1a	14	9	26	47
1b	53	56	30	36
1c	33	35	8	17

This problem of stage 94 can be overcome if the larval production was estimated using length data. More exact information or knowledge of the larval hatching length is then needed.

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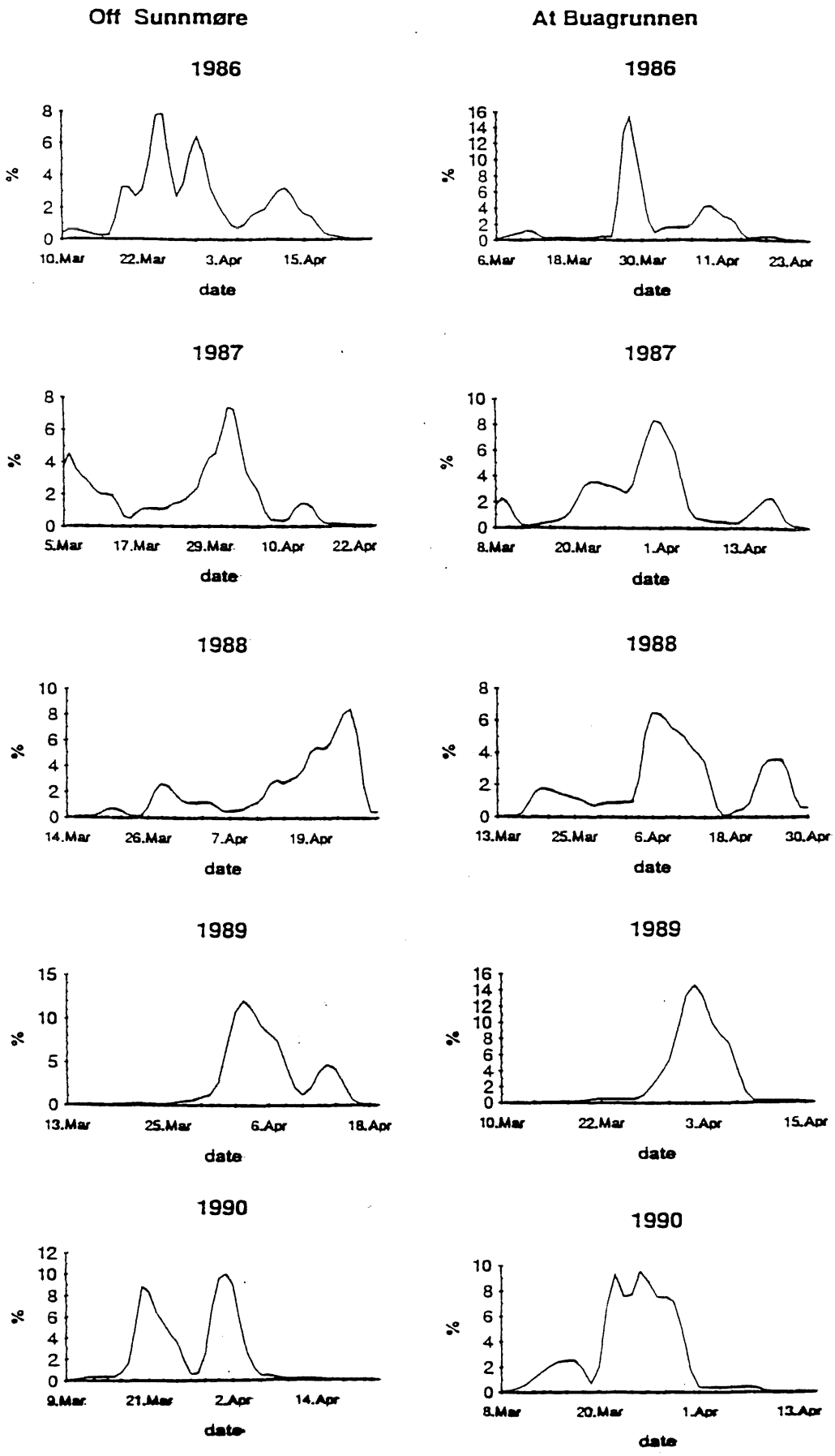

Fig.1 The hatching curves of the Norwegian spring-spawning herring off the Norwegian west coast in 1986-1990.