ABSTRACT

Spawning intensity measurements have been executed in Lofoten each year since 1976. They consist of egg net samples at selected spawning sites. In 1983, in addition, four quasi-synoptic egg surveys were conducted during the spawning season covering the total spawning area in Lofoten. These data are used to estimate the egg production during the spawning season 1983. The estimates are done by two methods. In the first method stage 1, 2 and 3 cod eggs are used in each survey to get 3x4=12 estimates of the egg production per day at different times during the spawning season. The 12 values are used to construct an egg production curve for the spawning season. The curve is integrated to get an estimate of the total egg production. By the other method certain assumptions about the egg distribution field have to be done, and the total egg production is computed by combining the spawning intensity data with one quasi-synoptic survey. The first method is the most correct one. The second method is more rapid and needs less ships time and time for egg analysis. It is discussed how to get the second method more accurate.
INTRODUCTION

Estimating the size of spawning stocks by computing the total egg production contains a number of problems which often is quite different for the different stocks. It is obvious that the methods and the field strategy should be quite different when estimating spawning stocks of demersal and pelagic spawners. But the problems may also be quite different for species of pelagic spawners with respect to the extent of the spawning area, spawning period, spawning behaviour, vertical distribution of the eggs, transport pattern of the eggs, characteristic concentrations and characteristic gradients of the eggs, mortality of the eggs, presence of other particles which may cause clogging of the sampling device, fecundity, and sex frequency of the stocks. All these variables should be considered when designing an egg-survey.

The cod spawning in Vestfjorden is extremely concentrated. Within an area of less than 6,000 km$^2$ more than 50 per cent of the Arcto-Norwegian cod spawns. The maximum concentration of cod eggs (found by traditional sampling device) may reach 15,000 per m$^2$ surface (Sundby 1980). This is quite different from the North Sea mackerel which cover a spawning area of approximately 250,000 km$^2$ and seldom reach concentrations of more than 1000 eggs per m$^2$ surface (Iversen 1981). The cod eggs are found in a very narrow zone in the cold outflowing Vestfjord-water close to Lofotveggen. The distribution of the eggs is, to a certain extent, dependent on the wind conditions. Northeasterly wind, which causes downwelling at Lofotveggen, concentrates the older stages towards the shore, while southwesterly wind, causing upwelling spread the eggs out towards the central part of Vestfjorden (Furnes and Sundby 1981). The spawning which occurs near the bottom in the transition layer between the upper cold coastal water and the atlantic water beneath cause an opposite distribution of the newly spawned eggs. During upwelling the cod spawn at shallow depths close to the shore, while during downwelling the cod spawns at greater depths off shore (Ellertsen et al. 1981). The distributions described above are qualitatively illustrated in Fig. 1.
Fig.1. Two typical situations during spawning in Lofoten. Left: downwelling. Right: Upwelling. A: Newly spawned eggs. B: Old eggs.

The eggs ascend from the spawning depth (50–150 m depth) with velocities between 0.2 and 1.5 mmsec$^{-1}$. The highest concentration of the eggs are found in the surface layer, but due to the high degree of turbulence in the wind mixed layer eggs are found down to more than 50 m depth. At higher wind speeds (>10 ms$^{-1}$) the eggs are almost homogeneous distributed in the upper layer (Solemdal and Sundby 1981, Sundby 1983).

Spawning intensity measurements have been made at three important spawning sites each year since 1975. These shows that the spawning starts during the first days of March and lasts until the last days of April. Maximum spawning intensity occurs during the first week of April (Solemdal, Sundby and Bratland 1983). These features seems to be very constant from year to year, and may lead to the conclusion that the cod spawning period is independent of physical and biological conditions of the sea water.
MATERIALS AND METHODS

The material consists of four quasi-synoptic egg-surveys, and spawning intensity measurements taken approximately twice a week all through the spawning season at three important spawning sites.

EGG SURVEYS

Fig. 2, 3, 4, 5 show the cruise tracks of the four egg surveys. At each station pelagic eggs were sampled with a traditional egg net (0.5 and 0.25 m$^2$ opening and 375 μ mesh size), and a C.T.D.-station was taken. At the first survey the egg net was hauled from 50 m depth to the surface. At the other surveys it was hauled from 75 m depth. The effective filtration through the nets are not 100%. Comparisons with integrated pump profiles during egg and larvae surveys during the years 1977, 1979, 1981, 1982 and 1983 in March–May, indicate a mean filtration efficiency of about 55% (Solemdal and Ellertsen, in press). The larger part of the stations was identical with the standard stations used by the Cod Larvae Project since 1977. The distance between the stations in each section varies from 9 km to 1 km. Close to the shore the distance between the stations is small to map the large concentrations and the large lateral gradients. In addition to the standard section, selected stations were also taken between each section. The distance between stations long-shore is considerably larger than the distance between the stations cross-shore because characteristic gradients of the egg concentration are approximately 10 times larger cross-shore than long-shore. The spawning area was divided in 6 sub areas shown in Fig. 6. Table 1 shows the number of stations taken at each cruise. The largest number of stations were taken in sub area II and III where the heaviest spawning occurs. Sub area VI was not covered during the first cruise due to the weather conditions. In the second survey sub area I was not covered, and in the third survey subarea V and VI were not covered.
Fig. 2. Cruise tracks 15–17 March 1983.

Fig. 3. Cruise tracks 21–25 March, 1983.
Fig. 4. Cruise tracks 25–27 March, 1983.

Fig. 5. Cruise tracks 8–11 April, 1983.
Fig. 6. Area of investigations divided in six sub areas.

Table 1. Number of egg net- and C.T.D.-stations in the sub areas for the four quasi-synoptic surveys in 1983.

<table>
<thead>
<tr>
<th>Subarea Cruise</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
<th>VI</th>
<th>SUM</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. 15-17 March</td>
<td>3</td>
<td>28</td>
<td>29</td>
<td>19</td>
<td>13</td>
<td>0</td>
<td>92</td>
</tr>
<tr>
<td>2. 21-25 March</td>
<td>0</td>
<td>28</td>
<td>33</td>
<td>22</td>
<td>25</td>
<td>20</td>
<td>128</td>
</tr>
<tr>
<td>3. 25-27 March</td>
<td>6</td>
<td>20</td>
<td>33</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>69</td>
</tr>
<tr>
<td>4. 8-11 April</td>
<td>8</td>
<td>28</td>
<td>34</td>
<td>22</td>
<td>15</td>
<td>19</td>
<td>126</td>
</tr>
</tbody>
</table>

The cod egg concentrations (numbers per m$^2$) of the stages 1, 2 and 3 were plotted in horizontal maps, and the isolines of the concentrations drawn. The egg numbers were integrated for each sub area by using a planimeter on the isolines.

The cod eggs were classified in six developmental stages, according to the system of Westernhagen (1970), modified by Strømme (1977), using 3 temperatures during incubation, 2.5, 4.0 and 5.0°C.
To check the duration of the three stages in situ experiments were carried out at the central spawning area at Hølla from the 26 March 1983. Artificially fertilized eggs were transferred to three glass jars with plankton net at the top and lowered to depths of 1-4, 55 and 120 meters. With intervals the jars were hauled and the development stage of the egg determined. Temperature profiles were recorded by Neill Brown CTD microprofiler.

The temperature in the upper 50 meters, where the majority of the eggs are distributed (Solemdal and Sundby 1981), is rather homogeneous with a mean of 3.0°C.

Parallel series with the same eggs were also run at 3.0°C in the refrigerator-room of the research vessel.

At 3°C the duration of stage 1 was 48 hours from fertilization including stage I aβ (Westernhagen 1970). The egg stage 2, from I aγ including I bβ, is from 2.0-4.38 days, and stage 3, from I bγ including II β, is from 4.38 to 7.0 days old. These values correspond fairly well with those cited from Strømme (1977). For the calculations the in situ values are used.

The identification of the eggs are routinously visual and performed onboard. The identifications are based on size, pigmentation etc. Early stages of cod and haddock eggs are impossible to separate, and difficulties also occur to separate cod eggs from eggs of saithe and Norway pout. To check the visual identifications special samples were frozen in liquid nitrogen and analyzed by a biochemical method, isoelectric focusing (Mork et al. 1983). The samples were taken in areas where mixing of different species usually occurs. Specially the relatively high egg densities on the south-eastern side of the Vestfjord, the inside of Lofotodden and the area off Lofoten have been sampled for biochemical identification. These areas are best shown in Fig. 16.

In Table 2 the results of eggs first visually identified as cod eggs and afterwards identified by isoelectric focusing are shown.
Table 2. Egg samples from three parts of the investigated area visually determined as cod eggs and checked by a biochemical method (Mork et al. 1983).

<table>
<thead>
<tr>
<th>Date</th>
<th>Area</th>
<th>Identification method</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Visual cod eggs</td>
<td>Biochemical cod</td>
<td>Biochemical haddock eggs</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Nos.</td>
<td>eggs</td>
<td></td>
</tr>
<tr>
<td>22 March</td>
<td>South East</td>
<td>15</td>
<td>15</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Vestfjord</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11 April</td>
<td>South East</td>
<td>56</td>
<td>53</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Vestfjord</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22 March</td>
<td>Inside</td>
<td>6</td>
<td>6</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lofotodden</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11 April</td>
<td>Off Lofoten</td>
<td>86</td>
<td>85</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sum</td>
<td>163</td>
<td>159</td>
<td>4</td>
</tr>
</tbody>
</table>

As shown in the table 98% of the cod eggs are correctly identified by the visual method.

SPAWNING INTENSITY STATIONS

As mentioned above the spawning intensity investigation were made at three of the main spawning sites: Austnesfjorden and Høllå in subarea II, and Henningsværstraumen in subarea III. The sampling was made with an egg net of 0.25 m$^2$ opening hauled from 100 m depth. Three stations were taken in Austnesfjorden, five stations at Høllå and four stations at Henningsværstraumen. Fig. 6 shows the position of the stations.

COMPUTING THE EGG PRODUCTION

The concentration of eggs per unit surface of stage $n$ on a spawning field may be expresses $C_n(x,y,t)$ where $x$ and $y$ represents the geographical coordinates and $t$ time. To compute the total production of eggs per time unit on a spawning field $f(t)$ the total area is integrated for each of the egg stages. This may be formalized mathematically:
\( f(t - \frac{\tau_n + \tau_{n+1}}{2}) = \int \int_{x,y} \frac{1}{\tau_{n+1} - \tau_n} c^n(x,y,t) \, dx \, dy \)

where \( \tau_n \) is the time of egg stage \( n \) to start.

To get a numerical expression for eq. 1 the first approximation is to assumed that the quasisynoptic egg survey is conducted at a fixed point of time, \( t_1 \). This approximation should be valid if the time change of the egg production is small compared to the duration of the survey. The concentration field \( c^n(x,y) \) obtain during one quasisynoptic survey is then integrated. In this work the three youngest egg stages are used. The egg production, \( f(t) \), then may be computed at three points of time

\[
 t_1 - \frac{\tau_1 + \tau_2}{2}, \quad t_1 - \frac{\tau_2 + \tau_3}{2}, \quad \text{and} \quad t_1 - \frac{\tau_3 + \tau_4}{2}.
\]

The four quasisynoptic surveys conducted during the spawning season 1983 therefore give \((4 \times 3) = 12\) egg production estimates at different times.

The total egg production during the spawning period, \( T \), is obtained by time integrating eq. 1.

\[
 F = \int_{T} f(t - \frac{\tau_n + \tau_{n+1}}{2}) \, dt = \int \int \int_{x,y} \frac{1}{\tau_{n+1} - \tau_n} c^n(x,y,t) \, dx \, dy \, dt
\]

The total number of eggs spawned during the spawning season is here computed in two ways:

1) In the first method the twelve egg production estimates from the synoptic surveys are used to construct a spawning period curve as shown in Fig. 10. The peak spawning and the end of the spawning is poorly covered by the synoptic surveys, and therefore the results from the spawning period stations are used to adjust the curve for those periods. At last the continuous curve is time integrated.

2) In the second method the spawning intensity curve is applied in a more direct way. Here the spawning intensity curve is time
integrated, and the level of this curve is determined by results from a synoptic survey. Thus one estimate is obtained by applying only one synoptic survey. From the present data twelve separate estimates of the total egg production may be obtained. The method is based on the assumption

\[ \frac{C(t)}{f(t)} \approx \text{const.} \]

where \( C(t) \) is the mean concentration of eggs found at the spawning period stations. This means that the spawning intensity stations is supposed to be representative for the whole spawning area. It implies that the egg distribution field is constant with respect to time, only the concentration varies with the spawning intensity.

Thus the time dependent distribution field may be written

\[ C(x,y,t) = C(t) \cdot c(x,y) \]

where \( C(t) \) is described by the spawning intensity curve and \( c(x,y) \) is described by the quasi-synoptic egg surveys.

RESULTS

THE FOUR QUASI-SYNOPTIC SURVEYS

Fig. 7, 8 and 9 show characteristic distributions of stage 1, 2 and 3 cod eggs in Lofoten. The highest concentrations are found in sub areas II and III where the spawning period stations are located (Fig. 6). Besides in a small area in sub area VI also high concentrations are found.

The change of egg distribution from stage 1 to stage 2 and stage 3 is typical: Older stages are found in a larger area indicating the influence of advection and diffusion. The distribution of eggs of higher stages than 3 are normally found in an area larger than that covered by the cruise. Therefore they are not included in these estimates.
Fig. 7. Distribution of stage 1 cod eggs, numbers per m$^2$, 21–25 March 1983.

Fig. 8. Distribution of stage 2 cod eggs, numbers per m$^2$, 21–25 March 1983.
In addition to the high concentrations of cod egg at the north-west side of Vestfjorden also some small concentrations of cod eggs are found in a narrow zone at the south-east side of Vestfjorden. These concentrations are not included in the estimates because it probably origins from coastal cod spawning. Investigations from earlier years show that these typical distributions partly extends into the fjords at the south-east side of Vestfjorden. However, the contribution to the total egg production in Lofoten is small, the order of less than 5%.

Based on the four synoptic cruises, and the three youngest stages the mean egg production per day was computed for twelve point of time according to eq. 1. These results are shown in Table 3. The table also includes results from a minor survey conducted during 23-25 February, when spawning was at its very start. In those cruises, where some of the sub-areas were not covered (see Table 1), the egg production was estimated by taking the fraction of egg production from the cruises where all sub-areas were covered.
Table 3. Estimated cod egg production per day $\times 10^{-9}$ in Lofoten based on four quasi-synoptic surveys and three egg stages. The data are also plotted in Fig. 10.

<table>
<thead>
<tr>
<th></th>
<th>21 Feb.</th>
<th>23 Feb.</th>
<th>10 March</th>
<th>13 March</th>
<th>15 March</th>
<th>18 March</th>
<th>20 March</th>
</tr>
</thead>
<tbody>
<tr>
<td>26.4</td>
<td>20.9</td>
<td>110.0</td>
<td>129.1</td>
<td>158.2</td>
<td>221.3</td>
<td>206.4</td>
<td></td>
</tr>
<tr>
<td>20 March</td>
<td>22 March</td>
<td>23 March</td>
<td>25 March</td>
<td>3 April</td>
<td>6 April</td>
<td>8 April</td>
<td></td>
</tr>
<tr>
<td>276.5</td>
<td>407.3</td>
<td>496.5</td>
<td>672.7</td>
<td>747.5</td>
<td>737.3</td>
<td>530.7</td>
<td></td>
</tr>
</tbody>
</table>

In Fig. 10 the data from Table 3 are plotted versus time. The spawning intensity data indicate that the peak spawning occurred between 25 March and 3 April. As already mentioned the largest spawning occurs in sub-area II and III. In Fig. 11 the egg production in sub-areas II and III is plotted versus time. The other curve in Fig. 10 represents the egg production in sub-areas I, IV, V and VI. About 70% of the egg production occurs in sub-areas II and III. Spawning outside this area is more evenly distributed over the spawning period. Fig. 12 indicates more detailed how spawning goes on in the four most important sub-areas. This shows that the peak spawning occurs at different time in each sub-area. The spawning seems to increase first in the outer regions. In sub-area IV a peak is seen 15 March. In the inner parts (sub-area II) the peak spawning occurs 25 March. Then the peak spawning towards the outer regions shows a time lag; sub-area III 3 April, sub-area IV after 8 April. In sub-area VI very few data exists. However, the spawning here seems to be independent of the spawning in the inner sub-areas.

THE SPAWNING INTENSITY MEASUREMENTS

Fig. 13 shows the mean concentration of newly spawned cod eggs (0–2 days old) from the 12 spawning intensity stations shown in Fig. 6. The stations are located in the central spawning areas in sub-area II and III. Therefore, it more or less shows the same features as curve no. 1 in Fig. 11, which represents the total spawning in sub-areas II and III. However, after the peak
Fig. 10. Estimates of egg production, numbers per day, based on the four quasi-synoptic surveys and stage 1, 2 and 3-eggs.

Fig. 11. Estimates of egg production, numbers per day, in sub areas II and III, and in sub areas I, IV and VI.
Fig. 12. Estimates of egg production, numbers per day, in sub area II, III, IV and VI.

Fig. 13. Mean concentration of stage 1 cod eggs from the 12 spawning intensity stations (shown in Fig. 6) during the spawning season 1983. Dotted line: Mean concentration of stage 1 cod eggs from the spawning intensity stations for the mean year 1976-1983.
Fig. 14. Distribution of stage 1 cod eggs, numbers per m$^2$, 8–11 April 1983.

Fig. 15. Distribution of stage 2 cod eggs, numbers per m$^2$, 8–11 April 1983.
spawning, 3 April, the spawning intensity stations show a very rapid drop while the synoptic survey no. 4 show that the spawning still is very high. This is explained by the special kind of egg distribution at that time. This is shown by Fig. 14, 15 and 16. The highest concentration is found off shore outside the spawning intensity stations.

COMPUTING THE TOTAL EGG PRODUCTION

The total egg production will here be computed in two ways as mentioned above.

Method 1) is based on the data from the synoptic surveys. The peak spawning and the end of the spawning is adjusted by applying the spawning intensity curve. This is shown in Fig. 10. Integrating this curve gives the total estimate of the egg production during the spawning season, shown in Table 4. About 70% of the total egg production occurs in sub-area II and III.
Method 2) relies on that the spawning intensity data (Fig. 13) represents the spawning intensity of the entire spawning area. However, it was shown above that the 1983 spawning curve does not represent the spawning of the total area, because of the off shore displacement of the spawning during the first days of April. Therefore the mean spawning curve during the years 1976–1983 is used to describe the spawning intensity for the total area. (Dotted line in Fig. 13.) Eq. (4) is then used for each synoptic survey and each of the three stages to get separate estimates of the egg production during the spawning season. The results are shown in Table 4.

Table 4. Total cod egg production \( \times 10^{-12} \) in Lofoten during the spawning in 1983.

<table>
<thead>
<tr>
<th>Method</th>
<th>Integrating the curve in Fig. 10</th>
<th>Applying eq. (4)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>March March March March March March March April April April</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10 13 15 18 20 22 23 25 3 6 8</td>
</tr>
<tr>
<td>Method 1</td>
<td>34.60 14.62 12.04 12.29 15.67 12.35 17.84 22.02 19.20 23.69 20.45</td>
<td></td>
</tr>
<tr>
<td>Method 2</td>
<td>19.82</td>
<td>Mean 18.62</td>
</tr>
</tbody>
</table>

DISCUSSION

In the present work 0–7 days old eggs divided in three stages has been used to compute the daily egg production. It has been assumed that the egg mortality is negligible in this period. Several authors have suggested that egg mortality may be considerable, e.g. mortality may be caused by the physical strain on the eggs by breaking waves. Pommeranz (1972) made thorough experiments on the effect of physical strain on plaice eggs, but he was not able to conclude that breaking waves would cause mass mortality of eggs. Besides only a small fraction of pelagic eggs are found in the top layer during stormy weather (Sundby 1983). Nevertheless mortality of eggs may also be caused by other reasons. However, the mortality of Arcto-Norwegian cod eggs is most probably on a rather low level. This is indicated by the results from the synoptic surveys, because the total production per day based on stage 3 eggs corresponds fairly well with
the production based on stage 1 eggs from the previous cruise (Fig. 10).

To compute the total egg production during the spawning season two methods have been used. The first method is simply based on integrating the data from quasi-synoptic egg surveys. This is obviously the most correct way of estimating the egg production because the total spawning area is covered for each survey. However, large effort has to be put into making synoptic surveys all through the spawning season. It is time consuming both with respect to ships time and analyzing time of the large number of egg samples. In the present investigation four synoptic surveys were made, but even this large effort was not enough to cover the total spawning period. The egg production more or less had to be guessed for the late interval of the spawning period (dotted lines in Figs 10 and 11).

In the second method it is assumed that the concentration of eggs from certain selected spawning period stations represents the spawning in the whole spawning area, i.e. it is assumed that the time variation of the spawning is equal at every spawning field. In this way the total egg production may be estimated in a cheap way based on one or two quasi-synoptic surveys combined with the spawning intensity curve (Fig. 13).

However, the assumptions made above that spawning intensity is equal at every point is not right, as shown by Fig. 11. Spawning outside the main spawning areas II and III is not that concentrated with respect to time. Besides special physical events, such as upwelling, may cause a different distribution of the eggs. This occurred during the fourth quasi-synoptic survey causing an anomalous drop of the egg concentration on the spawning period stations. Since the peak spawning, and the start and the end of the spawning in Lofoten is rather constant each year, the mean spawning intensity curve is supposed to give a better description of the spawning intensity than the data from 1983. The results in Table 4 are based on the mean spawning intensity curve for the years 1976–1983. The results seem to
correspond fairly well with those obtained by the first method when using the quasi-synoptic survey conducted during the peak spawning. The results from the first cruises does not correspond that well, probably because of the mismatch of time between the mean spawning period curve and the synoptic surveys. However, at the time of the peak spawning the spawning intensity flattens out for a short time. Therefore, the mean spawning period curve combined with two or three synoptic survey around the peak spawning time should be a reasonable alternative to the more elaborating and time consuming first method.

REFERENCES


