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Exploration of the Sea


# REPORT OF THE STUDY GROUP ON THE FECUNDITY OF SOLE AND PLAICE IN SUB-AREAS IV, VII, AND VIII 

Lowestoft, 6-10 July 1992

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## 1. PARTICIPATION AND TERMS OF REFERENCE

At the 1991 Statutatory Meeting in the La Rochelle (C.Res. 1991/2:15) it was decided that the "Study Group on the Fecundity of Plaice and Sole in Subareas IV, VII and VIII will meet in Lowestoft from 6-10 July 1992 to
a) analyse the egg production of sole in Sub-area IV, Divisions VIIa,d-e;
b) analyse the fecundity-length relations of sole in Sub-area IV, Divisions VIIa,d-g, and Sub-area VIII;
c) investigate the determinacy of fecundity in sole;
d) estimate the female spawning stock biomass of sole in 1991.

The meeting was attended by the following persons:

| C. Annand | Canada |
| :--- | :--- |
| F.A. van Beek | Netherlands |
| M. Giret | France |
| M. Greer Walker | England |
| R.S. Millner | England |
| A.D. Rijnsdorp (chairman) | Netherlands |
| P.R. Witthames | England |

Although not able to participate in the Working Group meeting, indispensable contributions were made by Dr U. Damm (Cuxhaven, F.R.Germany) and Dr R. de Clerck (Oostende, Belgium).

## 2. INTRODUCTION

Population assessments based on fishery-dependent information have become less reliable over the last decade due to uncertainties about the actual level of commercial landings as well as their age-composition (Anon, 1992). The ICES North Sea Flatfish Working Group, therefore, emphasized the need for fishery independent data sets on the trends in stock abundance such as bottom trawl surveys and egg surveys. Available Bottom Trawl surveys carried out annually to estimate the relative abundance of plaice and sole are (1) the UK ground fish survey which provides information on plaice since 1977; (2) the International Beam Trawl Survey which presents information on the abundance of sole and plaice in the southern North Sea (since 1985), eastern English Channel (since 1989), Bristol Channel and Irish Sea. These surveys can give an estimate of the abundance of the age-groups dominating the population, but may be less suitable to estimate the abundance of the older age-groups and thus of the total adult population. Abundance of the total adult population may be estimated from the total egg production through plankton surveys, providing an opportunity to validate the VPA.

A first internationally coordinated egg survey has been carried out in the North Sea in 1984 and 1985 (Anon, 1986). Further surveys in the North Sea were carried out by The Netherlands in 1988, 1989 and 1990 (van Beek, 1989; van der Land, 1991), and in the Bristol Channel by the UK in 1989 and 1990 (Horwood, 1992, in prep). A second internationally coordinated survey was organized in 1991 covering the North Sea and the eastern and western English Channel (VIId and VIIe).

Alongside the egg survey in 1991, a research program was scheduled to study the comparative fecundity in the different geographical areas, and to study the determinacy and atresia, in order to allow the estimation of the spawning stock biomass of sole in the different areas (Anon 1991). In this working group report the results of the fecundity studies and of the 1991 Sole Egg Survey as well as the previous egg surveys carried out in North Sea and English Channel are presented and the results of the
fishery-dependent and fishery-independent spawning stock biomass estimates are compared and discussed.

## 3. EGG SURVEYS

Different subpopulations of sole can be distinguished on the basis of tagging data and the spatial distribution of eggs (Anon 1989; Rijnsdorp et al. 1992). For the present analysis eight spawning areas were distinguished (Figure 3.1.), six areas in the North Sea and one area in the eastern and western English Channel, respectively. The 1991 sole egg survey covered all eight areas. Previous egg surveys were carried out in the North Sea in 1984, 1985, 1988, 1989 and 1990 (Anon, 1986; van Beek, 1989; van der Land, 1991), in the eastern English Channel in 1984 (Anon, 1986) and in the Bristol Channel in 1989 and 1990 (Horwood in prep). The results of the 1991 survey as well as the previous surveys in the North Sea and English Channel are (re)analysed in this report.

### 3.1. METHODS

Information on survey periods, sampling intensity, sampling areas and laboratories involved is given in Table 3.1.1. The survey grid was designed in accordance to the expected distribution in time and space, with a higher sampling intensity in the areas of expected egg production. The survey grid used the ICES rectangle as a basis, which was divided into 2,4 or 8 parts.

For the North Sea the station grid and timing followed the Planning Group of the 1984 International Sole Egg Survey (Anon, 1983, 1986) although some modifications were made. Based on the information of the distribution of sole eggs in 1984, the number of hauls in later surveys were reduced by excluding large areas with zero catches from the original station grid and by reducing the number of hauls in low density areas. Sampling of the estuarine areas in the Waddensea and Scheldt estuary was also abandoned in later years, despite the often high numbers of sole eggs, since the contribution of these areas to the total egg production is rather small due to the relatively small surface area of the estuaries.

The timing of the surveys in 1988 and 1989 was similar to 1984. From these surveys it became apparent that the timing of spawning can differ substantially between years and extra cruises were introduced in 1990 and 1991 in March. Surveys from 1988 onwards also comprised an additional July cruise to sample egg production of mackerel and/or horse mackerel.

In the North Sea the plankton sampling was similar in all years and was carried out with a Torpedo/DG III as described in detail in Anon (1983, 1986). The volume of water filtered was measured with a current meter mounted in the net opening. A mesh size of $500 \mu \mathrm{~m}$ was used in order to avoid clogging of the net with Phaeocystis. Plankton samples were fixed in 4\% buffered formaldehyde solution.

In VIId a modified Gulf 111 sampler of 50 cm internal diameter with a $19 / 20 \mathrm{~cm}$ diameter nose cone and $420 \mu \mathrm{~m}$ mesh plankton net. Each sample consisted of one or more double oblique hauls from the surface to as close to the bottom as possible at a standard towing speed of 5 knots. The dive profile was monitored and the descent and ascent maintained at approximately 1 m in 10 secs. Samples were washed from the net into a collecting bag and fixed in formaldehyde made up to a strength of $4 \%$ using distilled water.

In VIIe a Bongo net (Smith, 1974) was used during the first and third survey in 1991. This gear, equiped with two nets of $3-\mathrm{m}$ and towed at a speed of $2.5-3$ knots, allows to filter a larger volume of water compared to the Torpedo. The mean volume filtered during these two surveys was $345 \mathrm{~m}^{3}$. The two mechanical flowmeters - one for each net - have been calibrated in free flow in a circulating water channel, but no
calibration of the net itself has been done. Mesh size was $320 \mu \mathrm{~m}$ in survey A and 500 $\mu \mathrm{m}$ in survey C. During survey B a modified Gulf III sampler with a $500 \mu \mathrm{~m}$ mesh size was used similar to the one used in the North Sea.

At each station one oblique haul (single or double) was made from the surface to about $5-\mathrm{m}$ above the sea bed, filtering at least $50 \mathrm{~m}^{3}$ water. Water depth and the temperature were recorded at each station. In the North Sea, temperature was recorded at the surface, at $5-\mathrm{m}$ depth and at the bottom. In VIId, an integrated temperature over the water column was recorded, while in VIIe the surface temperature was recorded.

Plankton samples were sorted in the laboratory. In a few cases the catch was subsampled before sorting out. Egg stage was determined according to Riley (1974). No correction was made for the efficiency of the samplers, thus assuming that the efficiency was $100 \%$.

For each station the number of eggs $\left(\mathrm{N}_{\mathrm{i}}\right)$ of stage i were calculated per $\mathrm{m}^{2}$ and converted into a number per $\mathrm{m}^{2}$ per day using the developmental time ( $\mathrm{d}_{\mathfrak{j}}$ ) calculated according to the formulae given by Anon (1986) (Table 3.1.2.). For each area $j$ the production ( $\mathrm{P}_{\mathrm{i}}$ ) was calculated according to

$$
P_{i}=S_{i} N_{i} d_{i}^{-1}
$$

where $S_{i}$ is the surface of the area.
For each survey we further calculated the midpoint of sampling (days after 1 January) as the average day number, and the average temperature weighted over the number of eggs (stage 1-4), representing the ambient temperature for the average egg during a survey. The temperature used in the calculations was that recorded at the surface (VIIe), at 5-m depth (North Sea) and an integrated temperature over the water column (VIId).

Missing stations were extrapolated from the $\mathrm{N}_{\mathrm{i}}$ values of surrounding stations. If a larger area was not sampled the observed ${ }_{\mathrm{a}} \mathrm{P}_{\mathrm{i}}$ in survey $a$ was raised using a raising factor based on information from a previous or successive survey $b$. The raising factor was calculated as the ratio of the total egg production in survey $b$ over the production in survey $b$ of the sub-area which was sampled in survey $a$. In the presentation of the results both the extrapolated data and the basic observations will be given. Details of the extrapolations will be specified below.

### 3.2. SPATIAL DISTRIBUTION OF EGGS

## North Sea

The spatial distribution of stage-I eggs in the North Sea is shown in Fig. 3.2.1. 3.2.5. for each of the survey years respectively. The plots were produced using the SAS package available at the Fishery Laboratory in Lowestoft. The bubbles represent numbers under $1 \mathrm{~m}^{2}$ and are plotted on the exact position where the hauls were made. They are proportional to their value in the range of 1-20 eggs. $\mathrm{m}^{-2}$. Larger numbers are indicated with a fixed bubble size. Stage 1 eggs are about 1 days old and thus reflect the spawning areas of the sole stock.

The distribution of the stage 1 eggs appears to be similar in different years. The plots clearly show that the major spawning areas are restricted to a coastal band of $30-$ 40 miles off the coast. In the southern North Sea, south of $52^{\circ} 30^{\prime} N$, where the distance between the English and continental coast becomes smaller, spawning takes place all over the area. North of $52^{\circ} 30^{\prime} \mathrm{N}$, spawning is much more abundant and extends to a higher latitude along the continental coast as compared to the UK coast. Within the spawning area along the coast often high concentrations of eggs are observed in the Thames estuary, along the Belgian coast and along the Wadden islands.

## Eastern English Channel (VIId)

The abundance of stage 1 sole eggs as numbers $\mathrm{m}^{-2}$ for each survey is shown in Fig. 3.2.6 and 3.2.7 for 1984 and 1991, respectively. In the first survey of 1991 (middate 24 March), spawning had already begun along the French coast from the Baie de Somme northwards towards the North Sea. During the second cruise, there was extensive spawning along the English coast east of the Isle of Wight with high abundance levels ( $>20 \mathrm{~m}^{-2}$ ) in the Dover Strait. Spawning was at a low level and confined mainly to the eastern end of the Channel in the 3rd and 4th surveys and there was no sample with egg abundance above $15 \mathrm{~m}^{-2}$. In all 4 surveys, spawning was shown to be concentrated in the coastal rectangles. Spatial distribution of sole eggs in 1984 did not differ substantially from 1991.

## Western English Channel (VIId)

The abundance of stage 1 sole eggs as numbers $\mathrm{m}^{-2}$ for each survey is shown in Fig. 3.2.8. In the first cruise (mid-date 1 March), spawning had started in a large area in the offshore waters without distinct areas of high production. In the second survey in late March only the northern part of VIIe could be sampled due to bad weather, showing highest egg production in coastal stations. In the third survey in the second half of April, centres of high egg production occurred on both the UK and French coasts, with generally lower egg production in offshore stations.

### 3.3. EGG PRODUCTION

North Sea
The egg production was calculated for each of the six standard areas distinguished in the North Sea (\#1-\#6; Fig.3.1) from the egg production $\mathrm{m}^{-2}$.day ${ }^{-1}$ and the surface areas of the stations sampled. Surface areas used were similar to the ones used previously in analysing the 1984 survey (Anon, 1986). The distribution maps of egg production show that in some surveys one or more ICES rectangles within the standard areas \#1-\#6 were left unsampled. The production in these areas was extrapolated from the relative production of the sampled area in an other survey (see 3.1). A summary of the surveys used for the extrapolations is given in the following text table.

| year | survey | area (\#) | extranolation from |
| :--- | :---: | :---: | :--- |
| 1984 | A | 2 | 1984 B 2 |
| 1984 | A | 6 | 1984 B 6 |
| 1984 | C | 2 | 1984 B 2 |
| 1984 | D | 1 | 1984 C 1 |
| 1984 | D | 5 | 1984 C 5 |
| 1984 | D | 6 | 1984 C 6 |
| 1988 | D | 1 | zeros |
| 1988 | D | 3 | zeros |
| 1989 | A | 2 | 1989 B 2 |
| 1989 | A | 3 | 1989 B 3 |
| 1989 | E | 2 | zeros |
| 1990 | A | 2 | 1990 B 2 |
| 1990 | A | 3 | 1990 B 3 |
| 1991 | A | 1 | zeros |
| 1991 | A | 2 | zeros |
| 1991 | A | 5 | zeros |


| 1991 | A | 6 | zeros |
| :--- | :--- | :--- | :--- |
| 1991 | B | 6 | zeros |
| 1991 | C | 6 | 1984 B 6 |
| 1991 | D | 3 | 1991 E 3 |
| 1991 | D | 4 | 1991 E 4 |
| 1991 | D | 6 | 1984 C 6 |
| 1991 | E | 6 | 1984 D 6 |

The production estimates for each survey including the surface areas sampled ( $10^{-}$ ${ }^{3} \mathrm{~km}^{-2}$ ), the mid-day of the survey (calculated as the average day number of the samples with 1-Jan = day 1 ), and the mean temperature at $5-\mathrm{m}$ depth weighted over the abundance of sole eggs (ambient temperature) is given in Tables 3.3.1.- 3.3.5. In these Tables, the production estimates excluding extrapolations, those including small extrapolations and those including the large extrapolations specified in the text table, are given expressed in $10^{-9}$ eggs day ${ }^{-1}$.

## Eastern English Channel (VIId)

All four egg surveys carried out in this area in 1991 were complete and no extrapolations were necessary. Results are given in Table 3.3.6. The seasonal production curves show a distinct peak in egg production in survey $C$.

## Western English Channel (VIId)

Survey A and C in the western English Channel were complete except for the two most western stations which were missed in the survey A. The production of these stations was assumed to be equal to the two neighbouring stations to the east which showed a similar level of egg production in survey $C$. To provide an estimate for the large unsampled area in survey B a ratio was calculated from survey A. Because these two surveys were separated by only 20 days and the mean surface temperatures were nearly the same, it was considered that this selection was appropriate. The sampled area comprised $23.4 \%$ of the production of the total area in survey A and the observed eggproduction in survey $B$ was raised by a factor $100 / 23.4=4.3$. The results including the extrapolations is given in Table 3.3.7.

### 3.4. TIMING OF THE SPAWNING

The seasonal production curves are shown by area in Figure 3.4.1.- 3.4.6. indicating differences in the time of spawning between areas as well as between years. Under the assumption that the egg production is normally distributed in time a parabolic regression was fitted through the observed logged production values. The peak in egg production was found by setting the first derivate $\mathrm{dY} / \mathrm{dt}=0$. Thus, given the parabole $\log _{\mathrm{n}} \mathrm{N}=\mathrm{a}+\mathrm{bt}+\mathrm{ct}^{2}$ - the peak in egg production ( $\mathrm{t}_{\text {max }}$ ) can be calculated as $\mathrm{t}_{\text {max }}=$ $\mathrm{b} / 2 \mathrm{c}$. The parameters b and c were estimated from a GLM analysis of the pooled data set of North Sea, western and eastern English Channel employing the model:

$$
\begin{aligned}
& \mathrm{Y}=\mathrm{a}+\left(\mathrm{b}_{\text {common }}+\mathrm{b}_{\text {area }}+\mathrm{b}_{\text {year }}\right) \mathrm{t}+\left(\mathrm{c}_{\text {common }}+\mathrm{c}_{\text {area }}+\mathrm{c}_{\text {year }}\right) \mathrm{t}^{2}+ \\
& \text { STAGE + AREA + YEAR + AREA.YEAR + STAGE.AREA.YEAR. }
\end{aligned}
$$

The factor AREA coded for eight areas, YEAR for five years and STAGE for three egg stage 1,2 and $3+4$. Egg stages 3 and 4 were pooled because these sometimes occurred in very low numbers in the AREA. YEAR cells.

The full model explained $78 \%$ of the total variance in egg numbers. Backward stepwise analysis revealed that the interaction between STAGE.AREA.YEAR was not significant ( $\mathrm{F}_{54,191}=0.76$ ) indicating that the decline in egg numbers during incubation did not differ significantly between areas and years. The significant interaction between Area. Year ( $\mathrm{F}_{16,245}=3.88 ; \mathrm{P}<0.01$ ) indicated that egg numbers differed between areas as well as between years. The above model assumes that egg production follows a normal distribution in time. The results for stage 1 eggs in 1991, which are shown as an example in Fig 3.4.7, suggest that the assumption is reasonable.

Estimates of the time of peak spawning in Table 3.4.1 and Fig.3.4.8 show that spawning moves progressively northwards in time, but that the timing differs substantially between years. Spawning was relatively late in 1984 and relatively early in 1989-1990. Temperature curves for these years recorded at a coastal station in the southern North Sea (Fig.3.4.10) indicates that the delay in spawning in 1984 coincided with a relatively cold water temperatures in March and April. The advanced spawning in 1989 and 1990 coincided with relatively warm water temperatures in winter. Average temperatures recorded in the standard areas during the cruises are given in Table 3.4.2 and shown for 1991 in Fig.3.4.9. As with the differences in the timing of spawning across years, the differences between the timing of spawning across areas seems to be related to the temperatures prior to spawning. The dashed horizontal line at $9^{\circ} \mathrm{C}$ in Fig.3.4.9 marks the peak of spawning in the western English Channel and southern North Sea, but peak spawning seems to occur at a slightly higher temperature in more northern areas. The ambient temperature observed across years and areas, indicating the temperature at which an average egg developed during the total spawning period, appears to be rather constant (Table 3.4.3). These results suggest that sole adjust their spawning time according the temperature conditions in sea.

### 3.5. PRODUCTION OF FERTILIZED EGGS

## Determining the start and end date of spawning

The seasonal production of the various stages in the different areas was calculated by trapezoidal integration. To this end a start and end date of spawning had to be determined. Since, in a number of cases the first of last survey showed a high level of egg production, the assumed start or end date will have a substantial effect on the estimated total production. Therefore, we have used the information on the timing of the egg production obtained from the GLM parabolic regression lines of section 3.4. to estimate the start and end of spawning. The GLM model yields an objective estimate of the time of peak spawning based on the observed production values of stage 1,2 , and $3+4$ eggs, and can be used to estimate the start and end of the spawning period if the time period of spawning is known. Inspection of the observed egg production curves in Fig. 3.4.1-3.4.6 suggests that the time period over which egg production occurred was about 120 days, and the start and end of the spawning period were estimated at $\mathrm{t}_{\max }-60$ and $\mathrm{t}_{\max }+60$ days respectively.

## Cumulative egg production

Table 3.5.1. summarizes the production of stage $1,2,3$ and 4 eggs in the different areas, as well as the number of fertilized eggs estimated by the intercept at $t=0$ of the linear regression of $\log _{n}$ numbers against the mean age $(t)$ of the different stages. This approach assumes that egg mortality is constant during incubation. In order to obtain an estimate of the production of fertilized eggs for larger areas, we did not just add the estimated egg production values for the different areas, since the estimate of the production of fertilized eggs is dependent on the mortality of eggs. It was prefered to sum the production figures by stage first and then calculate the intercept at $t=0$ of the linear regression of $\log _{\mathrm{n}}$ numbers against t. The results, given in Table 3.5.2, show that the egg production of fertilized eggs decreased since 1984 and showed a fourfold increase between 1989 and 1990. In 1991 the egg production slightly decreased. Comparison of the level of egg production in the North Sea and Channel indicates that the latter is about $10 \%$ (VIId) and $5 \%$ (VIIe) of the level in the North Sea.

The accuracy of the estimated production of fertilized eggs is dependent on the slope of the linear regression. Fig.3.5.1 shows that the assumption of a constant mortality during incubation may not hold, since the decline between stage 1 and stage 2 eggs is generally smaller than that between the other egg stages. Employing the mortality rate between stage 1 and stage 2 would have reduced substantially the estimated production of fertilized eggs. It is difficult to envisage which factors may cause the mortality to be much lower during the early developmental stages compared to that in the later stages. Egg mortality curves for other species with pelagic eggs, e.g.plaice (Harding et al, 1978a, 1978b; Heessen and Rijnsdorp, 1990) and cod (Daan, 1981) generally do not show a discrepancy from the assumed constant mortality. One possible factor may be the developmental time used. If the distinction of developmental stages differ between live and fixed material, the parameter estimates used in the present study may not be valid since these were based on live material (Riley, 1974; Anon, 1986).

In the North Sea, the estimated production of fertilized eggs are underestimates because the egg production of the estuaries were not sampled (1988 and later) or not included in the analysis (1984).

## 4. FECUNDITY

Fecundity estimates were presented from eight separate sole stocks covering a geographic area from Portugal to the north east coast of England. All the samples were collected during the same calendar year (1991) and the same methods and analyses were used in each case. It is therefore possible for the first time to compare the fecundities of different sole stocks across the greater part of the range of this species in European waters.

The eight sampling sites together with the date of capture are shown in Fig 4.1. Ovaries were dissected out of the fish prior to spawning, fixed in buffered formalin and returned to the laboratory. Prior to processing the volume of the ovary was measured (Scherle, 1970) and a transverse section was cut out from the mid-point of each of the lobes and placed in a histological cassette. Following dehydration the tissue was embedded in historesin and sectioned at $4 \mu \mathrm{~m}$ in a refrigerated cabinet $\left(-4^{\circ}\right)$ using a motorised microtome. The sections were stained with periodic acid Schiffs (Khoo, 1979). Those ovaries containing post-ovulatory follicles or hydrated oocytes were rejected.

A stereological method (Emerson et al. 1990) employing a weibel grid and point and profile counts was used to estimate the number of vitellogenic oocytes. All the oocytes which showed the PAS stain were counted and it was assumed that the sole was a determinate spawner, that is, the number of vitellogenic oocytes prior to spawning (potential annual fecundity) represented the number of eggs spawned (true
annual fecundity) apart from losses through atresia. Oocytes showing alpha atresia were recognised because of an irregular or pitted zona pellucida and a disorganised ooplasm. They were counted as part of the stereological analysis. The size of oocytes was estimated by selecting oocytes where the central nucleus was present and taking the mean of measurements across two axis taken at right angles. A correction was made to take account of changes in nuclear diameter and oocyte diameter during growth.

### 4.1. FECUNDITY - BODY SIZE RELATIONSHIPS

### 4.1.1. DATA OF 1991

The relationships between fecundity - length and gutted weight for the eight geographic areas are shown in Figs 4.1.1 and 4.1.2, respectively. A comparison of the length and weight relationships using an ANCOVA is shown in Fig 4.1.3 and a comparison by area at a length of 37 cm is tabulated. The IVB east and IVC were not significantly different and the results from these two areas were combined. Similarly the results from VIIe, VIII and IXa were not significantly different and have been combined. The average fecundity of the latter samples was approximately half that of samples from IVb and IVc. The average fecundity from areas VIIa, VIId and IVb west showed values between these two extremes. The regression parameters of the fecundity - length and fecundity - body weight relationships for the pooled samples from areas which were not significantly different are given in the text tables below.

| 1991 data | $\ln$ Fecundity $=\alpha+\beta \ln \mathrm{L}$ |  | Fecundity $=\alpha \mathrm{W}^{\beta}$ |  |
| :---: | :---: | :---: | :---: | :---: |
|  | $\alpha$ | $\beta$ | $\alpha$ | $\beta$ |
| IVb (east) \& IVc | -1.285 | 4.014 | -30068 | 1084 |
| VIIa \& VIId | -1.559 | 4.014 | -61527 | 975.5 |
| IVb (west) | -1.805 | 4.014 | 69503 | 838.3 |
| VIIe, VIII, \& IX | -1.974 | 4.014 | -17683 | 626.1 |
|  | $\ln$ Fecundity $=\alpha+\beta \ln L$ |  | $\ln$ Fecundity $=\alpha+\beta \ln \mathrm{W}$ |  |
| VIId (1988-91) | -2.373 | 4.25 | 5.619 | 1.176 |
| VIIb (west) | -2.578 | 4.25 | 4.495 | 1.323 |

### 4.1.2. ANNUAL VARIATION IN FECUNDITY

Fecundity data was available for the period 1988 to 1991 in two areas, IVb west (the Flamborough Off ground) and VIId and this data was used to examine year to year differences in fecundity between the two areas.

The relationship between fecundity and gutted weight for each year and area is shown in Fig. 4.1.4 and 4.1.5 and the coefficients for the regression lines are given in Table 4.1.2.1. There are no clear trends in either slopes or intercepts with time, although in IVb there was a marked increase in the slope in 1989 and 1990. The main area difference was a shallower slope and higher intercept in VIId except in 1988. This suggests that the sole in VIId produce more eggs for their body weight than the IVb west fish but the discrepancy decreases as the fish increase in weight.

In order to see whether the area or year differences were significant, an analysis of variance was carried out and the results are shown in Table 4.1.2.2. The model testing for different slopes in each area had a significance of $\operatorname{Pr}>\mathrm{F}=0.0153$ indicating that there were significant differences between the fecundities in the two areas. When
different slopes between years was examined across areas, there was no significant difference ( $\mathrm{Pr}>\mathrm{F}=0.0827$ ).

The results suggest that over a period of 4 years,year to year variation in fecundity is less important than area differences and that a mean value for fecundity in each area can be used to estimate total egg production, if no relevant annual figure is available.

### 4.2. DETERMINACY OF FECUNDITY

Current methods of assessment using plankton surveys and fecundity estimates assume that the sole has a determinate fecundity. In other words the potential annual fecundity counted prior to spawning is equivalent to the number of eggs spawned less any losses through atresia. The argument concerning determinacy has centred upon the presence of a hiatus in the oocyte size frequency distribution between the previtellogenic and the vitellogenic oocytes. If a hiatus is present in sole prior to spawning it is generally accepted that previtellogenic oocytes would not become vitellogenic during the current spawning season. However the absence of a hiatus is not proof of an indeterminate fecundity and measurement of oocyte growth rates in this context would be useful. Earlier work has shown that a hiatus exists in the size frequency distribution of sole from ICES areas VIIf (Horwood and Greer Walker, 1990) and VIId (Greer Walker and Witthames, 1990). However, Urban and Alheit (1988) have argued on the basis of a continuous oocyte size frequency distributions that the sole has an indeterminate fecundity. In the present work size frequency distributions are presented from sole during the first half (Fig 4.2.1) and two thirds of the way through (Fig 4.2.2) the spawning season. A definite hiatus is apparent in 8 of the 13 sole examined.

A second line of investigation adopted by the working group was to compare the annual egg production from the product of the batch fecundity and the number of batches produced in the spawning season with the annual fecundity estimated from stereological analysis (section 4.1). The batch fecundity was measured by counting the number of hydrated oocytes in spawning ovaries (Fig 4.2.3). The batch fecundity was calculated to be 8400 , SE 1363 oocytes (mean fish length 31.6 cm ) which is similar to Urban's (1988) estimate of 7600 , SE 1035 (mean fish length 31.4 cm ) for the same area. The frequency of batch production was calculated from the incidence of fresh post-ovulatory follicles in histological sections. Tank experiments at Lowestoft designed to estimate the duration of fresh post ovulatory follicles in the ovary by monitoring the condition of the nuclei indicate the stage duration to be in the region of $6-12 \mathrm{~h}$. On the basis of the abundance of fresh post ovulatory follicles in the ovaries of a random sample of spawning fish the batch frequency was shown to be a minimum of 2 days (and this result is not at variance with tank experiments (Houghton et al , 1985). The length of time spent in spawning condition (maturity stages $5 \& 6$ ) was calculated to be 60 days (section 4.4). The product of the number and size of egg batches gives a fecundity of 252000 ; this compares with the measured potential fecundity of 298000. However, this latter figure includes some oocytes which will later become atretic. These results are consistent with sole from IVb east having a determinate spawning strategy.

We conclude on the available evidence that sole from IVB east have a determinate fecundity because:

1. A hiatus develops in the oocyte size frequency distribution between previtellogenic and vitellogenic oocytes in the majority of spawning fish examined.
2. Calculations of batch size, batch frequency and length of the spawning season point to a determinate fecundity.
3. Sole from areas VIId and VIIf have a determinate fecundity and it would be unlikely, bearing in mind the low level of interchange required to produce genetic homogeneity among stocks, that sole from IVb east would be different.

### 4.3. Atresia

The prevalence and intensity of alpha atresia found in the fecundity samples from ICES area IV, VII and VIII are shown in Table 4.3.1. The samples from area IXa were excluded from this analysis because it is difficult to distinguish between autolysis and atresia in a market sample. The results from area VIla are particularly high (prevalence $69 \%$, intensity $7.6 \%$ ) and as the samples were collected in Liverpool bay the possibility of pollutants as the cause is under investigation. The prevalence of atresia in the remainder of the samples varied between 4 and $18 \%$ and the intensity in the individual ovaries varied between 2 and $8 \%$. The intensity of atresia during spawning in sole from IVb east reached a peak between half and three-quarters of the way through spawning and subsequently declined (Table 4.3.1).

It appears that the smaller vitellogenic oocytes around 200 mm in diameter become atretic during the earlier part of spawning. It is difficult to measure the size of these oocytes precisely because they have no nucleus and are irregular in shape, therefore, the size distribution of these oocytes shown in Fig 4.3.1 is probably overextended. One of the effects of the smallest vitellogenic oocytes becoming atretic is to extend the hiatus in the size frequency distribution between previtellogenic and vitellogenic oocytes as spawning progresses. Larger atretic vitellogenic oocytes in the size range $400-600 \mathrm{~mm}$ are confined to a period about two-thirds of the way through spawning and this is reflected in a high intensity of atresia at this time (Table 4.3.1). Large atretic oocytes are rarely found in the ovary at any other time during spawning and towards the end of spawning alpha atresia is uncommon. There seems therefore to be two stages in the regulation of fecundity by means of atresia. The reduction in number of the smallest vitellogenic oocytes in the early part of the spawning season and secondly the reduction in the number of larger vitellogenic oocytes towards the end of the spawning season.

The effect of the loss of atretic oocytes through spawning on the predicted fecundity of sole in area IVb east.

The spawning period was divided into three parts and it was assumed that the eggs were shed at a uniform rate. The tumover rate of atretic oocytes was taken to be 10 days; a rate similar to that found in anchovy (Hunter and Macewicz, 1985) and cod (Kjesbu et al 1991).

The mean loss from the annual fecundity was calculated as: $\mathrm{P} \times \mathrm{I} \times \mathrm{T}$, with $\mathrm{P}=$ prevalence, $\mathrm{I}=$ mean intensity ( $\log$ transformed x duration of the spawning stage) and $\mathrm{T}=$ turnover rate of atretic oocytes ( 10 days). The total number of atretic oocytes produced during the spawning season corresponds to $8.5 \%$ of the annual fecundity.

| Progress through spawning | Duration (days) | Mean loss <br> from <br> annual fecundity (\%) |
| :---: | :---: | :---: |
| Prespawning-50\% full | 30 | 4.6 |
| 50\%-25\% full | 15 | 2.7 |
| 25\%-0 spent | 15 | 1.2 |
| Total | 60 | 8.5 |

### 4.4. DURATION OF MATURITY STAGES

The rate of development of the ovary through the successive maturity stages was estimated using market sampling data collected by The Netherlands during the period 1970-1979. This market sampling programme comprises length-stratified samples taken monthly from commercial landings. At the laboratory length, weight, ovary weight, age, and maturity were recorded. Maturity stages 1-8 were given according to the description in Anon (1991). Stage-1 represent immatures; stage 2-3 early developing fish; stage-4 late developing fish; stage 5-6 spawning fish; and stage 7-8 spent fish.

Figure 4.4.1. shows the frequency distribution of the maturity stages by month for the Southern Bight (IVc) and German Bight (IVb east) separately. In order to restrict the analysis to adult females, only 5 -years old and older fish were included. Spawning stages 5 and 6 dominate the female population in the months April-May in the Southern Bight and in May in the German Bight. After the spawning period, the proportion of spent fish (stage 7-8) quickly increased to about $70 \%$ in July and August. In late summer the spent stages returned to maturity stage 2 and 3. From December onwards the ovary again developed into stage 4. A comparison of the Southern and German Bight indicates that spawning starts earlier in the Southern Bight. The transition of fish through the other non-spawning maturity stages does not indicate a substantial difference between the two areas.

In Figure 4.4.2. the cumulative proportions of maturity stages within the adult population (age group $5+$ ) are shown. The ascending lines, which connect the cumulative proportions of the successive maturity stages ( $2,2+3,2+3+4$, etc.), demonstrate the transition of adult fish through the successive maturity stages. The arrow dissecting the ascending lines at $50 \%$, indicates the time-period during which the average female is in spawning condition. The stage duration can be estimated from the time period between the points at which the dashed $50 \%$ line dissects the ascending lines. Thus estimated, females are on average in maturity stage- 4 for two to three months in the Southern and German Bight respectively; and two months in stage 5-6. Figure 4.4.3. shows the results of a more detailed analysis of the spawning stages 5-6 for the spawning period 1 March - 30 June, employing a time interval of 10 days (1-10, 11-20 and 20-30) instead of one month. This analysis indicates that the spawning duration in the Southern and German Bights is approximately 60 days from 1 April-1 June in the Southern Bight and from 15 April-15 June in the German Bight.

### 4.5. EGG NUMBERS AND EGG SIZE

Egg number and egg size are two intimately linked parameters that are related to the reproductive investment of a fish. Given a certain amount of resources available, a fish can make either a small number of large eggs or a large number of small eggs. Egg size is generally seen as an adaptive trait to the feeding conditions for larvae (Bagenal, 1971). In North Sea plaice, changes in the fecundity-body size relationship have been observed since 1900 that were not reflected in the ovary size - body size relationships, suggesting a constant reproductive investment but a difference in the trade-off between egg numbers and egg size (Rijnsdorp, 1991). These considerations raises the question as to whether the observed differences in fecundity in sole between geographical areas are related to differences in egg size.

One possible approach to this problem is to measure egg size from plankton samples. Since egg size decreases over the spawning season (Bagenal, 1971; Rijnsdorp and Jaworski, 1990), egg measurements should be collected over the total spawning season in order to allow estimation of the overall mean egg size by weighting over the seasonal production curve. This approach has been explored using plankton samples collected in 1989, 1990 and 1991 in three areas: 1) in the inner German Bight. 2) off
the Belgian coast - Scheldt estuary and 3) on the UK coast of VIId. For each of the samples the mean egg size and its SE are plotted against day number since 1 January, showing a decrease in egg size over the spawning season. The slope of the decrease in egg size however is steeper in the German Bight. No difference in egg size is suggested between the samples collected off the Belgian coast and in VIId. For the 1991 data a weighted average egg size was calculated for the German Bight and the Belgian coast. Table 4.5.1. shows that the weighted average egg size in the German Bight was 1.083 mm compared to 1.211 mm off the Belgian coast, a difference of $10 \%$. The difference in the the cube of the radius, which is approximately representative for the reproductive investment or weight of the eggs, shows a difference of $40 \%$. This difference in egg volume compares to a difference in relative fecundity between VIId and IVb-east of about $30 \%$, suggesting that the reproductive investment in energetic terms is roughly similar. An independent check on this inference can be made from a comparison of the ovary weight - body size relationships between both areas.

This exploratory analysis indicates that a study of egg sizes is an indispensable part of the study of fecundity. A practical implication might be that if the reproductive investment between areas and years is constant, differences in fecundity can be approximated from differences in egg size determined from plankton samples.

## 5. VPA ESTIMATE OF SPAWNING STOCK BIOMASS

Female spawning stock biomass of sole was estimated for 1991 based on the fishing mortalities and stock numbers from the sexes combined VPA (Anon, 1992), an average sex ratio observed in the second quarter landings, and an average proportion of maturity-at-age. It was further assumed that the level of fishing mortality in 1991 was equal to the level in 1990. The stock numbers at 1 April was calculated from the numbers at 1 January assuming that $0.25 \times(\mathrm{F}+\mathrm{M})$ had occurred. Basic data for the calculations are given in Table 5.1.1, 5.1.3 and 5.1.4 for the North Sea and VIId and VIIe, respectively. The sex ratio used for North Sea sole was a smoothed mean ratio observed in the second quarter landings in the period 1985-1989. The maturity-at-age array was the average proportion females of maturity stage $>=3$ observed in the market sampling data for the period 1982-1991. For both Channel areas, sex ratios were smoothed averages observed in second quarter landings over a number of years in the 1980s. The maturity-at-age array was estimated from market samples taken in the second quarter. The thus calculated spawning stock biomass and the corresponding age composition is shown in Table 5.1.2-5.1.4.

## 6. COMPARISON OF SSB ESTIMATES OF VPA AND EGG SURVEYS.

The estimates of the fertilized egg production from plankton surveys were converted into an estimate of the spawning stock biomass using appropriate data on the fecundity per gram of body weight (relative fecundity) in each area. In section 4.1 it was shown that the fecundity-body weight relationships differed significantly between the western English Channel (\#8), the eastern English Channel (\#7), the German Bight (\#2,3,4) and Flamborough (\#6).

Fecundity in the southern North Sea (Belgian coast and Thames estuary) were assumed to be similar to that in the eastern English Channel (VIId). The assumption is supported by the following two observations: 1 - egg sizes were similar in the eastern

Channel (\#7) and the southern North Sea (\#1, Belgian coast); 2 - midwater trawling showed that soles migrate through the Strait of Dover between the southern North Sea and the eastern English Channel (Greer Walker and Emerson, 1989), suggesting that from the both spawning populations in the southern North Sea and eastern Channel sole mix on the feeding grounds during summer.

Since the relative fecundity increases with body weight, the value representative for the population (relative population fecundity) will be affected by the age composition of the population. Therefore, the relative population fecundity was calculated taking account of the age structure and the observed weight-at-age array. The following text table shows the effect of the varying age structure and weight-at-age on the relative population fecundity.

This text table also summarizes the production estimates of fertilized eggs from section 3 and gives the corresponding spawning stock biomass estimates employing the appropriate relative population fecundities. In 1989 and 1990 the egg surveys did not cover areas \#5 and \#6 and the SSB estimates are as a consequence minimum estimates only. Comparison of the VPA and the egg survey estimates of SSB shows that the egg survey estimate is generally a factor two higher than the VPA estimate. Only in the 1988 and 1989 egg survey yielded a roughly similar SSB as the VPA.

|  | 1984 | 1988 | 1989 | 1990 | 1991 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Relative population fecundity (number of eggs per gram gutted body weight)North Sea |  |  |  |  |  |
|  |  |  |  |  |  |
| \#1,5 | 751 | 750 | 754 | 736 | 757 |
| \#2,3,4 | 975 | 974 | 974 | 963 | 981 |
| \#6 | 565 | 564 | 570 | 545 | 565 |
| English Channel |  |  |  |  |  |
| VIId (\#7) | - | - | - | - | 658 |
| VIIe (\#8) | - | - | - | - | 508 |
| Cumulative egg production ( $\times 10^{-12}$ ) from egg surveys |  |  |  |  |  |
|  |  |  |  |  |  |
| \#1 | 5.675 | 3.073 | 4.113 | 10.327 | 7.673 |
| \#1,5 | 10.069 | 7.059 |  | - | 11.847 |
| \#2,3,4 | 18.337 | 4.851 | 12.446 | 46.237 | 43.557 |
| \#6 | 3.613 | 0.264 |  | - | 3.326 |
| English Channel |  |  |  |  |  |
| VIId (\#7) | - | - | - | - | 4.556 |
| VIIe (\#8) | - | - | - | - | 2.791 |
| SSB estimates from egg surveys (thousand tonnes) |  |  |  |  |  |
| North Sea |  |  |  |  |  |
| \#1-6 | 38.6 | 14.9 | 18.2 | 62.0 | 65.9 |
| English Channel |  |  |  |  |  |
| VIId (\#7) | - | - | - | - | 6.9 |
| VIIe (\#8) | - | - | - | - | 5.5 |
| SSB estimate from VPA (thousand tonnes) |  |  |  |  |  |
| North Sea | 23.3 | 21.0 | 20.0 | 30.7 | 30.9 |
| English Channel |  |  |  |  |  |
| VIId (\#7) | - | - | - | - | 3.1 |
| VIIe (\#8) | - | - | - | - | 1.3 |

## Discussion

The discrepancy between egg surveys and VPA may be due to a number of factors related to both egg surveys and VPA. Although the time available to the Working Group did not allow a detailed analysis of the possible causes a preliminary overview of likely factors is given below.

VPA: 1 - the VPA estimate of SSB in the most recent years is highly dependent on the level of terminal fishing mortality. These estimates will become more reliable in the near future when the VPA will have converged. This will particularly affect the 1990 and 1991 estimate of SSB dominated by the very large 1987 year class; 2 - the absolute level of spawning stock biomass is affected by the level of natural mortality used in the calculations. In all stocks a level of $M=0.1$ is assumed although no firm empirical evidence is available to support this. 3 - absolute levels of SSB may be affected by the unreliability in the landings and corresponding age-compositions due to unreported and misreported landings; 4 - maturity: part of the females with maturity stage 3 , which were considered to be mature, may not have taken part in spawning (de Veen, 1970). A reduction of the proportion mature females, however, will lead to a decrease in the SSB estimate from the VPA and in an increase in the discrepancy.

Egg surveys: 1 - estimated number of fertilized eggs is highly dependent on the mortality in the egg stage; 2 - egg surveys did not cover the total spawning area (estuaries were excluded) and SSB estimate is a minimum estimate; 3 - extrapolations for missing stations in part of the cruises may have affected the SSB estimate. However, it is unlikely that this will have caused a systematic bias; 4 -actual fecundity may be $8 \%$ lower than the potential fecundity due to atresia, but correction for atresia will raise the SSB estimate from egg surveys thus increasing the discrepancy.

Horwood (1992) found that the egg surveys on sole in the Bristol Channel carried out in 1989 and 1990 yielded a SSB estimate about twice that of the VPA, a discrepancy similar to the results of our study. However, in North Sea plaice, Bannister et al. (1974) found that an egg survey estimate of SSB was substantially lower that the VPA estimate, a discrepancy also found by Heessen and Rijnsdorp (1990) with data for 1987 and 1988.

Although, the absolute level of SSB estimated by VPA was not validated by the egg surveys, the differences across years and areas do correspond. Fig. 6.1 shows the egg surveys, at least in the North Sea, are linearly related with the VPA estimates of SSB, but the two data points for the English Channel do not fall on the line. Although the relationship may change in the near future due to convergence of the VPA estimates of SSB, the qualitative agreement between both estimates support the conclusion that egg surveys can be used to provide fishery-independent estimates of the stock.

## 7 CONCLUSIONS AND RECOMMENDATIONS

### 7.1. CONCLUSIONS

1 - New evidence presented in this report supports the conclusion that sole is a determinate spawner throughout its geographical range.

2 - Fecundity was shown to increase gradually from about $500 \mathrm{egg} . \mathrm{g}^{-1}$ body weight in the southwestern areas (IX, VIII, VIIe-g) to almost twice that value in the eastern North Sea. Annual differences in fecundity-body size relationships were non-significant.

3 - Comparison of SSB estimates obtained independently from egg surveys and VPA indicated that in six out of eight comparisons, encompassing four stocks, the egg surveys gave an about two times higher SSB than the VPA surveys.

4 - Despite the discrepancy in absolute SSB estimate, the egg surveys give fisheryindependent information about the trends in spawning stock biomass that can be used to validate the trends obtained by VPA when uncertainties about the landing statistics continue to exist .

### 7.2. RECOMMENDATIONS

1. It is recommended that the international egg survey in the North Sea (IVc, IVb) and English Channel (VIId, VIIe) are continued in 1994 to provide a fishery independent estimate of the spawning stock biomass to validate the estimate obtained by VPA.
2. It is recommended that sole fecundity samples be collected and analysed during 1993 from ICES areas IVc west (Thames estuary) and IVc-east (Belgian coast) to determine the position of this area in the cline of a decreasing fecundity from southwest to northeast.
3. It is recommended that further samples of spawning sole be collected from the German Bight during January, February and March 1993 to study oocyte growth rates in the area with a view to confirm the determinacy of sole in this area.
4. It is recommended that further studies be made to elucidate the factors affecting fecundity in sole in order to understand variability in fecundity between areas and years and their possible relation with recruitment variability.
5. It is recommended that incubation experiments should be carried with sole eggs to determine the relationship between developmental rate after fixation and temperature to check the relationships determined in the early 1970s.
6. Further studies should be directed at the possible causes of the discrepancy between spawning stock biomass estimates obtained by VPA and egg surveys.

## References

Anon, 1983. Report of the Ad hoc Working Group on the feasibility of a sole egg survey in 1984. ICES C.M. 1983/G:4
Anon, 1986. Report of the ad hoc Working Group on the 1984 and 1985 sole (Solea solea L.) egg surveys. Lowestoft, 4-7 February 1986. ICES C.M. 1986/G:95
Anon, 1989. Report of the ad hoc study group on juvenile sole tagging. ICES C.M. 1989/G:21.
Anon, 1991. Report of the Study Group on the fecundity of sole and plaice. Lowestoft, 18-21 September 1990. ICES C.M. 1990/G:2.
Anon, 1992. Report of the North Sea Flatfish Working Group. ICES, 17-23 October 1991. ICES C.M. 1992/Assess: 6

Arbault, S. and Lacroix, N. 1975. Essais comparatifs des pouvoirs de capture deux filets plancton (Gulf III encased et Bongo).ICES C.M. 1975/J:8.
Bagenal, T.B. 1971. The interrelation of the size of fish eggs and the date of spawning. J. Fish Biol. 3: 207-219.

Bannister, R.C.A., Harding, D. and Lockwood, S.J. 1974. Larval mortality and subsequent yearclass strength in the plaice (Pleuronectes platessa L.). In The early life history of fish, pp 21-37 Ed. by J.H.S. Blaxter. Springer, Berlin.
Beek, F.A. van 1989. Egg production of North Sea sole in 1988. ICES C.M. 1989/G:45.
Cushing, D.H. 1975. Marine ecology and fisheries. Cambridge University Press, Cambridge. pp 1-278.
Daan, N. 1981. Comparison of estimates of egg production in the Southern Bight cod stock from plankton surveys and market statistics. Rapp. P.-v. Reun. Cons. int. Explor. Mer 178: 242-243.
Emerson, L.S., Greer Walker, M. and Witthames, P. R. 1990. A stereological method for estimating fish fecundity. J. Fish Biol. 36 721-730.
Greer Walker, M. and Emerson, L. 1990. The seasonal migration of soles (Solea solea) through the Dover Strait. Neth. J. Sea Res. 25: 417-422.
Greer Walker, M. and Witthames, P. 1990. The fecundity of sole (Solea solea L.) from ICES areas IVB in 1987 and 1988 and VIId in 1988. International Council for the exploration of the sea. Demersal Fish Committee CM1990/G:37 6pp.
Harding, D., Nicholls, J.H., Tungate, D.S. 1978a The spawning of the plaice (Pleuronectes platessa L.) in the southern North Sea and English Channel. Rapp. P.-v. Reun. Cons. int. Explor. Mer 172: 102-113.

Heessen, H.J.L. and Rijnsdorp, A.D. 1989. Investigations on egg production and mortality of cod (Gadus morhua L.) and plaice (Pleuronectes platessa L.) in the southern North Sea and English Channel. Rapp. P.-v.Reun.Cons.int.Explor.Mer 191: 15-20.
Horwood, J.W. 1992. A comparison of assessment methods: VIIf+g sole. ICES C.M. 1992/D:20.
Horwood, J.W. Sole in the Bristol Channel. Adv. Mar. Biol. in prep.
Horwood, J.W. and Greer Walker, M. 1990. Determinacy of fecundity in sole (Solea solea) from the Bristol Channel. J. mar. Biol. Ass. UK 70 803-813.
Houghton, R.G., Last, J.M. and Bromley, P.J. 1985. Fecundity and egg size of sole (Solea solea (L.)) spawning in captivity. J. Cons. int. Explor. Mer 42: 162-165.
Hunter, J.R. and Macewicz, B.J. 1984. Rates of atresia in the ovary of capture and wild northern anchovy Engraulis mordax. Fishery Bulletin 83 No 2. 119-136.
Jossi, J.W., Marak, R.R. and Peterson, H. 1975. At-sea data collecting and laboratory procedures.- Marmap survey J. Manual, Marmap Program Office. National Marine Fisheries Service edit., Washington.
Khoo, K.H. 1979. The histochemistry and endocrine control of vitellogenesis in goldfish ovaries. Can. J. Zool. 57 617-620.
Kjesbu, O.S., Klungsoyr J., Kryvi H., Witthames P.R., and Greer Walker M. 1991. Fecundity, atresia and egg size of captive Atlantic cod (Gadus morhua) in relation to proximate body composition. 48 No. 12. 2333-2343.
Land, M.A. van der. 1991. Distribution of flatfish eggs in the 1989 egg surveys in the southeastern North Sea, and mortality of plaice and sole eggs. Neth. J. Sea Res. 27: 277-286.
Rijnsdorp, A.D. 1991. Changes in fecundity of female North Sea plaice (Pleuronectes platessa L.) between three periods since 1900. ICES J. mar. Sci. 48: 253-280.
Rijnsdorp, A.D. and A. Jaworski, 1990. Size-selective mortality in plaice and cod eggs: a new method to study egg-mortality. J. Cons. int. Explor. Mer 47: 256263.

Rijnsdorp, A.D., van Beek, F.A., Flatman, S. Millner, R.M., Riley J.D., Giret M. \& de Clerck, R. 1992 Recruitment of solestocks, Solea solea (L.) in the Northeast Atlantic. Neth. J. Sea Res. (in press)
Riley, J.D. 1974. The distribution and mortality of sole eggs (Solea solea L.) in inshore areas. In The early life history of fish, pp 39-52 Ed. by J.H.S. Blaxter. Springer, Berlin.
Scherle, 19780. A simple method for volumetry of organs in quantitative stereology. J. micros 26 57-60.

Schnack, D. 1974. On the reliability of methods for quantitative surveys of fish larvae.In: J.H.S. Blaxter (ed.). The Early Life History of Fish. Springer-Verlag Berlin.
Sherman, K. and Honey A. 1971.- Size selectivity of the Gulf III and Bongo zooplankton Samplers.- I.C.N.A.F., Research bulletin, 8: 45-48.
Smith, E. 1974. Manual of methods for fisheries resource survey and appraisal.- Part 4, Standard techniques for pelagic fish egg and larva surveys.- National Marine Fisheries Service edit., Washington.
Urban, J. 1988. Vergleichende Fruchtbarkeitsuntersuchungen bei Scholle (Pleuronectes platessa L.) and Seezunge (Solea solea L.) PhD thesis. Free University of Berlin. 113 pp.
Urban, J. and Alheit, T. 1988. Oocyte development cycle of plaice Pleuronectes platessa and north sea sole, Solea solea. ICES C.M.1988/G:52. 8 pp .
Veen, J.F de., 1970. On some aspects of maturation in the common sole Solea solea (L.). Ber. dt. wiss. Kommn. Meeresforsch., 21 78-91.

Table 3.1.1. Summary of planktonic sampling in North Sea and eastern and western English Channel.

| Survey | Sub-areas <br> (\#) | Sampling period | Number of hauls all | Mid point (Jan 1st=1) | Countries |
| :---: | :---: | :---: | :---: | :---: | :---: |
| North Sea |  |  |  |  |  |
| 1984 |  |  |  |  |  |
| A |  | 27/3-5/4 | 114 | 91 | UK |
| B |  | 24/4-4/5 | 312 | 119 | BEL |
| C |  | 14/5-30/5 | 269 | 142 | NET |
| D |  | 14/6-5/7 | 236 | 174 | GER |
| 1988 |  |  |  |  |  |
| A |  | 5-12/4 | 56 | 99 | NET |
| B |  | 24/4-5/5 | 121 | 121 |  |
| C |  | 16/5-2/6 | 148 | 145 |  |
| D |  | 20-30/6 | 131 | 176 |  |
| E |  | 18-28/7 | 87 | 205 |  |
| 1989 |  |  |  |  |  |
| A |  | 10-18/4 | 55 | 105 | NET |
| B |  | 24/4-2/5 | 103 | 118 |  |
| C |  | 22/5-7/6 | 117 | 150 |  |
| D |  | 19/6-28/6 | 71 | 175 |  |
| E |  | 10-18/7 | 64 | 195 |  |
| 1990 |  |  |  |  |  |
| A |  | 12-15/3 | 65 | 73 | NET |
| B |  | 26-30/3 | 67 | 88 |  |
| C |  | 23/4-3/5 | 107 | 119 |  |
| D |  | 21/5-13/6 | 110 | 151 |  |
| E |  | 18/6-27/6 | 74 | 174 |  |
| F |  | 11/7-20/7 | 66 | 198 |  |
| 1991 |  |  |  |  |  |
| A |  | 18-21/2 | 39 | 51 | UK |
| B |  | 18-27/3 | 101 | 80 | NET |
| C |  | 12-26/4 | 141 | 110 | GER |
| D |  | 13-22/5 | 93 | 138 |  |
| E |  | 8-20/6 | 136 | 163 |  |
| F |  | 8-11/7 | 47 | 191 |  |

Eastern English Channel (VIId)

| 1984 |  |  |  |  |  |
| :--- | :--- | ---: | ---: | ---: | ---: |
| A | $\# 7$ | $27-29 / 3$ | 24 | 88 | UK |
| B | $\# 7$ | $24-26 / 4$ | 24 | 116 | BEL |
| C | $\# 7$ | $21-25 / 5$ | 22 | 144 |  |
| D | $\# 7$ | $17-19 / 6$ | 24 | 170 |  |
|  |  |  |  |  |  |
| 1991 | $\# 7$ | $20-27 / 3$ | 55 | 84 | UK |
| A | $\# 7$ | $12-18 / 4$ | 59 | 109 |  |
| B | $\# 7$ | $16-22 / 5$ | 58 | 136 |  |
| D | $\# 7$ | $31 / 5-7 / 6$ | 56 | 155 |  |

Western English Channel (VIIe)
1991

| A | $\# 8$ | $26 / 2-5 / 3$ | 84 | 61 | FR |
| :--- | :--- | ---: | ---: | ---: | ---: |
| B | $\# 8$ | $19-21 / 3$ | 32 | 80 |  |
| C | $\# 8$ | $18-24 / 4$ | 74 | 113 |  |

Table 3.1.2. Parameter estimates of the relationship between the stage duration of sole eggs ( D in days) and temperature $\left(\mathrm{T}\right.$ in ${ }^{\circ} \mathrm{C}$ ) according the model: $\mathrm{D}=\exp (\beta . \mathrm{T}+\alpha)$. Modified from Riley (1974) according Anon (1986).

|  | $\alpha$ | $\beta$ |
| :---: | :---: | :---: |
| stage 1 | 2.0193 | -0.123 |
| stage 2 | 1.4941 | -0.153 |
| stage 3 | 2.5075 | -0.151 |
| stage 4 | 1.4106 | -0.069 |

Table 3.3.1. Egg production of sole (numbers per day x 10-6) in the North Sea in 1984 and corresponding mid-points of the cruises and temperatures at 5 -m depth by survey and standard area \#1-\#6. Egg production was estimated from the observations only (sampled surface area; left), observations plus small extrapolations for a few missing stations (extrapolation rectangles; middle) and from observations plus extrapolations for unsampled areas including extrapolation areas; right).

| survey A | area | midday Temp number 5 -mtr |  | sampled surface area |  |  |  |  | including extrapolation rectangles |  |  |  |  | including extrapolation areas |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 1 | 90.8 | 11.2 | 13.1 | 5678 | stage 11 | 0 | 0 | Stare 13.8 | - 5678 | $\frac{250}{}$ | stage 0 | 0 | $\frac{13.8}{}$ | 5678 | 250 | 0 | 0 |
|  | 2 | 91.9 | 5.9 | 10.0 | 352 | 258 | 0 | 0 | 10.0 | 352 | 258 | 0 | 0 | 25.5 | 881 | 646 | 0 | 0 |
|  | 3 |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  |
|  | 4 |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  |
|  | 5 | 91.3 | 6.8 | 13.5 | 1542 | 860 | 103 | 0 | 13.6 | 1542 | 860 | 103 | 0 | 13.6 | 1542 | 860 | 103 | 0 |
|  | 6 | 91.6 | 5.6 | 6.1 | 0 | 0 | 0 | 0 | 6.1 | 0 | 0 | 0 | 0 | 26.8 | 0 | 0 | 0 | 0 |
| B | 1 | 116.7 | 9.6 | 12.6 | 58183 | 51012 | 9650 | 889 | 13.8 | 59086 | 51347 | 9746 | 889 | 13.8 | 59086 | 51347 | 9746 | 889 |
|  | 2 | 123.4 | 8.8 | 17.6 | 16260 | 19959 | 6879 | 1850 | 25.5 | 18758 | 22497 | 7605 | 2153 | 25.5 | 18758 | 22497 | 7605 | 2153 |
|  | 3 | 123.4 | 9.1 | 6.6 | 7306 | 752 | 12 | 0 | 6.9 | 8839 | 1389 | 61 | 0 | 6.9 | 8839 | 1389 | 61 | 0 |
|  | 4 | 119.7 | 8.4 | 23.2 | 1456 | 0 | 0 | 0 | 23.2 | 1456 | 0 | 0 | 0 | 23.2 | 1456 | 0 | 0 | 0 |
|  | 5 | 116.6 | 9.4 | 13.6 | 22395 | 9985 | 1058 | 8 | 13.6 | 22396 | 9985 | 1058 | 8 | 13.6 | 22396 | 9985 | 1058 | 8 |
|  | 6 | 118.2 | 8.0 | 26.7 | 6689 | 460 | 49 | 40 | 26.8 | 6842 | 460 | 49 | 40 | 26.8 | 6842 | 460 | 49 | 40 |
| C | 1 | 140.4 | 9.9 | 10.2 | 11543 | 18174 | 7287 | 3561 | 14.2 | 14311 | 21878 | 9716 | 4810 | 14.2 | 14311 | 21878 | 9716 | 4810 |
|  | 2 | 143.5 | 9.0 | 8.4 | 5730 | 14519 | 2324 | 780 | 12.0 | 7321 | 16042 | 3215 | 1166 | 25.5 | 21371 | 46830 | 9385 | 3404 |
|  | 3 | 137.5 | 8.4 | 3.2 | 14478 | 3613 | 2427 | 75 | 6.9 | 27747 | 6639 | 4520 | 211 | 6.9 | 27747 | 6639 | 4520 | 211 |
|  | 4 | 147.3 | 9.6 | 23.2 | 99587 | 67746 | 6008 | 780 | 23.2 | 99587 | 67746 | 6008 | 780 | 23.2 | 99587 | 67746 | 6008 | 780 |
|  | 5 | 139.1 | 9.5 | 13.5 | 28919 | 25754 | 7300 | 903 | 13.6 | 29770 | 25801 | 7301 | 903 | 13.6 | 29770 | 25801 | 7301 | 903 |
|  | 6 | 139.2 | 9.8 | 26.2 | 13626 | 7418 | 1500 | 342 | 26.8 | 14146 | 7702 | 1501 | 344 | 26.8 | 14146 | 7702 | 1501 | 344 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| D | 1 | 170.5 | 14.2 | 3.7* 2.4 | 5410 | 3996 | 385 | 0 | 2.4 | 5410 | 3996 | 385 | 0 | 14.2 | 16477 | 12170 | 1173 | 0 |
|  | 2 | 171 | 12.1 |  | 2545 | 1166 | 1195 | 0 | 3.7 | 2545 | 1166 | 1195 | 0 | 3.7 | 2545 | 1166 | 1195 | 0 |
|  | 3 | 170.3 | 12.6 | 5.5 | 8938 | 4199 | 3620 | 89 | 6.9 | 11927 | 7303 | 5299 | 259 | 6.9 | 11927 | 7303 | 5299 | 259 |
|  | 4 | . 173.1 | 12.8 | 23.2 | 46876 | 18556 | 16769 | 2000 | 23.2 | 46876 | 18556 | 16769 | 2000 | 23.2 | 46876 | 18556 | 16769 | 2000 |
|  | 5 | 176.9 | 14.1 | 7.9 | 1807 | 3662 | 638 | 112 | 7.9 | 1807 | 3662 | 638 | 112 | 13.6 | 2516 | 5098 | 888 | 156 |
|  | 6 | 174.5 | 10.9 | 15.6 | 15566 | 9082 | 3416 | 928 | 15.6 | 15566 | 9082 | 3416 | 928 | 26.8 | 27504 | 16047 | 6036 | 1640 |

Table 3.3.2. Egg production of sole (numbers per day $\times 10-6$ ) in the North Sea in 1988 and corresponding mid-points of the cruises ana temperatures at $5-\mathrm{m}$ depth by survey and standard area \#1-\#6. Egg production was estimated from the observations only (sampled surface area; left), observations plus small extrapolations for a few missing stations (extrapolation rectangles; middle) and from observations plus extrapolations for unsampled areas including extrapolation areas; right).


Table 3.3.3. Egg production of sole (numbers per day x 10-6) in the North Sea in 1989 and corresponding mid-points of the cruises and temperatures at $5-\mathrm{m}$ depth by survey and standard area $\# 1-\# 6$. Egg production was estimated from the observations only (sampled surface area; left), observations plus small extrapolations for a few missing stations (extrapolation rectangles; middle) and from observations plus extrapolations for unsampled areas including extrapolation areas; right).

| survey | area | midday number | Temp 5-mtr | sampled surface area |  |  |  |  | including extrapolation rectangles |  |  |  |  | including extrapolation areas |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| A | 1 | 107 | 8.9 | 14.0 | 48666 | 25010 | 12534 | 5231 | 14.0 | 48666 | 25010 | 12534 | 5231 | 14.0 | 48666 | 25010 | 12534 | 5231 |
|  | 2 | 101 | 7.4 | 11.2 | 9984 | 4028 | 2183 | 1654 | 13.1 | 15329 | 5273 | 2993 | 2882 | 25.5 | 16812 | 5783 | 3283 | 3161 |
|  | 3 | 101 | 6.6 | 4.0 | 630 | 4214 | 1956 | 71 | 4.0 | 630 | 4214 | 1956 | 71 | 6.4 | 852 | 5698 | 2645 | 96 |
|  | 4 |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  |
|  | 5 |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  |
|  | 6 |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  |
| B | 1 | 115 | 8.6 | 14.2 | 28996 | 26030 | 11834 | 7372 | 14.2 | 28996 | 26030 | 11834 | 7372 | 14.2 | 28996 | 26030 | 11834 | 7372 |
|  | 2 | 117 | 7.7 | 25.5 | 26139 | 16611 | 6768 | 2886 | 25.5 | 26139 | 16611 | 6768 | 2886 | 25.5 | 26139 | 16611 | 6768 | 2886 |
|  | 3 | 118 | 7.5 | 6.4 | 24642 | 10199 | 3773 | 724 | 6.4 | 24642 | 10199 | 3773 | 724 | 6.4 | 24642 | 10199 | 3773 | 724 |
|  | 4 | 118 | 7.0 | 13.7 | 40732 | 23436 | 8013 | 1315 | 23.2 | 63973 | 33542 | 10820 | 1721 | 23.2 | 63973 | 33542 | 10820 | 1721 |
|  | 5 |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  |
|  | 6 |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  |
| C | 1 | 143 | 13.0 | 14.1 | 16743 | 40731 | 13205 | 4385 | 14.1 | 16743 | 40731 | 13205 | 4385 | 14.1 | 16743 | 40731 | 13205 | 4385 |
|  | 2 | 147 | 12.7 | 20.0 | 12869 | 15930 | 4551 | 1671 | 25.3 | 12869 | 15930 | 4551 | 1671 | 25.3 | 12869 | 15930 | 4551 | 1671 |
|  | 3 | 150 | 12.1 | 6.7 | 18328 | 21766 | 2699 | 380 | 6.7 | 18328 | 21766 | 2699 | 380 | 6.7 | 18328 | 21766 | 2699 | 380 |
|  | 4 | 156 | 12.3 | 19.1 | 19590 | 24468 | 4455 | 1353 | 23.1 | 23010 | 30229 | 5000 | 1542 | 23.1 | 23010 | 30229 | 5000 | 1542 |
|  | 5 | 144 | 12.3 | 12.0 | 12840 | 10488 | 5068 | 2781 | 12.0 | 12840 | 10488 | 5068 | 2781 | 12.0 | 12840 | 10488 | 5068 | 2781 |
|  | 6 |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  |
| D | 1 | 179 |  | 12.6 | 0 | 0 | 0 | 0 | 13.6 | 0 | 0 | 0 | 0 | 14.2 | 0 | 0 | 0 | 0 |
|  | 2 | 175 | 15.1 | 20.0 | 435 | 0 | 409 | 0 | 25.5 | 435 | 0 | 409 | 0 | 25.5 | 435 | 0 | 409 | 0 |
|  | 3 | 172 | 15.0 | 6.4 | 2117 | 2266 | 798 | 0 | 6.4 | 2117 | 2266 | 798 | 0 | 6.4 | 2117 | 2266 | 798 | 0 |
|  | 4 | 172 | 16.8 | 21.5 | 7992 | 13780 | 6603 | 1171 | 23.1 | 8525 | 16678 | 8289 | 1345 | 23.1 | 8525 | 16678 | 8289 | 1345 |
|  | 5 |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  |
|  | 6 |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  |
| E | 1 | 198 |  | 14.2 | 0 | 0 | 0 | 0 | 14.2 | 0 | 0 | 0 | 0 | 14.2 | 0 | 0 | 0 | 0 |
|  | 2 | 193 |  | 18.9 | 0 | 0 | 0 | 0 | 22.5 | 0 | 0 | 0 | 0 | 25.5 | 0 | 0 | 0 | 0 |
|  | 3 | 192 | 16.8 | 6.4 | 422 | 0 | 0 | 0 | 6.4 | 422 | 0 | 0 | 0 | 6.4 | 422 | 0 | 0 | 0 |
|  | 4 | 192 | 16.7 | 16.6 | 1758 | 5268 | 477 | 0 | 23.5 | 3390 | 7044 | 795 | 0 | 23.5 | 3390 | 7044 | 795 | 0 |
|  | 5 |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  |
|  | 6 |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  |

Table 3.3.4. Egg production of sole (numbers per day $\times 10-6$ ) in the North Sea in 1990 and corresponding mid-points of the cruises and temperatures at $5-\mathrm{m}$ depth by survey and standard area \#1-\#6. Egg production was estimated from the observations only (sampled surface area; left), observations plus small extrapolations for a few missing stations (extrapolation rectangles; middle) and from observations plus extrapolations for unsampled areas including extrapolation areas; right).


Table 3.3.5. Egg production of sole (numbers per day x 10-6) in the North Sea in 1991 and corresponding mid-points of the cruises and temperatures at 5 -m depth by survey and standard area \#1-\#6. Egg production was estimated from the observations only (sampled surface area; left), observations plus small extrapolations for a few missing stations (extrapolation rectangles; middle) and from observations plus extrapolations for unsampled areas including extrapolation areas; right).

| year: 1991 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| survey | area | midday Temp number 5 -mtr |  | surface sampled surface area <br> stage I <br> stage II stage III stage IV |  |  |  |  | surface | including extrapolation rectangles stage I stage II stage III stage IV |  |  |  | surface | including extrapolation areas |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  | ge iv |  |
|  | 2 | 52 | 4.35 |  |  |  |  |  | 13.4 12.2 | 0 | 0 | 0 | 0 | 13.4 12.2 | 0 | 0 | 0 | 0 | 14.2 25.5 | 0 | 0 | 0 | 0 |
|  | 3 |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  |
|  | 4 |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  |
|  | 5 | 50 | 5.25 | 9.6 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 13.6 | 0 | 0 | 0 | 0 |
|  | 6 | 51 | 4.70 | 1.4 | 0 | 0 | 0 | 0 | 1.4 | 0 | 0 | 0 | 0 | 26.8 | 0 | 0 | 0 | 0 |
| B | 1 | 78 | 7.44 | 13.9 | 18536 | 6447 | 198 | 0 | 13.9 | 18536 | 6447 | 198 | 0 | 13.9 | 18536 | 6447 | 198 | 0 |
|  | 2 | 80 | 651 | 23.5 | 2722 | 193 | 100 | 0 | 25.3 | 2722 | 193 | 100 | 0 | 25.3 | 2722 | 193 | 100 | 0 |
|  | 3 | 80 |  | 5.5 | 0 | 0 | 0 | 0 | 6.7 | 0 | 0 | 0 | 0 | 6.7 | 0 | 0 | 0 | 0 |
|  | 4 |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  |
|  | 5 | 81 | 8.08 | 12.1 | 8883 | 6016 | 3447 | 507 | 13.8 | 9405 | 6545 | 3636 | 507 | 13.8 | 9405 | 6545 | 3636 | 507 |
|  | 6 | 79 |  | 20.8 | 0 | 0 | 0 | 0 | 20.8 | 0 | 0 | 0 | 0 | 26.8 | 0 | 0 | 0 | 0 |
| C | 1 | 106 | 9.00 | 13.8 | 52427 | 64866 | 31703 | 8521 | 14.1 | 52607 | 66742 | 32514 | 8656 | 14.1 | 52607 | 66742 | 32514 | 8656 |
|  | 2 | 110 | 8.02 | 23.7 | 64726 | 64612 | 24592 | 8537 | 25.5 | 64726 | 64612 | 24592 | 8537 | 25.5 | 64726 | 64612 | 24592 | 8537 |
|  | 3 | 113 | 7.92 | 6.7 | 24831 | 19886 | 7675 | 4315 | 6.7 | 24831 | 19886 | 7675 | 4315 | 6.7 | 24831 | 19886 | 7675 | 4315 |
|  | 4 | 114 | 7.48 | 21.7 | 43130 | 12003 | 801 | 755 | 21.7 | 43130 | 12003 | 801 | 755 | 21.7 | 43130 | 12003 | 801 | 755 |
|  | 5 | 106 | 8.76 | 13.5 | 31460 | 28736 | 6844 | 2094 | 13.5 | 31460 | 28736 | 6844 | 2094 | 13.5 | 31460 | 28736 | 6844 | 2094 |
|  | 6 | 107 | 6.61 | 20.8 | 2906 | 0 | 0 | 0 | 20.8 | 2906 | 0 | 0 | 0 | 26.8 | 4295 | 0 | 0 | 0 |
| D | 1 | 135 | 9.77 | 13.8 | 57834 | 71828 | 27975 | 10799 | 14.1 | 58739 | 72856 | 28340 | 11044 | 14.9 | 58739 | 72856 | 28340 | 11044 |
|  | 2 | 139 | 10.33 | 22.8 | 73493 | 60015 | 17279 | 7682 | 25.5 | 82137 | 73502 | 19264 | 8606 | 25.5 | 82137 | 73502 | 19264 | 8606 |
|  | 3 | 150 | 11.05 | 2.8 | 37559 | 43665 | 24225 | 7584 | 3.2 | 42588 | 46718 | 25180 | 7687 | 6.6 | 87768 | 96280 | 51893 | 15841 |
|  | 4 | 149 | 10.91 | 10.0 | 150999 | 157620 | 24974 | 7886 | 10.0 | 150999 | 157620 | 24974 | 7886 | 22.3 | 273308 | 285292 | 45203 | 14273 |
|  | 5 | 138 | 9.66 | 13.2 | 31149 | 21580 | 9156 | 3378 | 13.5 | 31890 | 21631 | 9156 | 3378 | 13.5 | 31890 | 21631 | 9156 | 3378 |
|  | 6 | 136 | 9.12 | 20.8 | 12040 | 11606 | 2914 | 677 | 20.8 | 12040 | 11606 | 2914 | 677 | 26.8 | 18734 | 18059 | 4534 | 1053 |
| $E$ | 1 | 161 | 12.30 | 13.9 | 13113 | 12232 | 4922 | 1575 | 14.1 | 13327 | 12467 | 4984 | 1575 | 14.1 | 13327 | 12467 | 4384 | 1575 |
|  | 2 | 169 | 12.39 | 25.5 | 11923 | 10668 | 3117 | 592 | 25.5 | 11923 | 10668 | 3117 | 592 | 25.5 | 11923 | 10668 | 3117 | 592 |
|  | 3 | 167 | 11.85 | 6.4 | 30215 | 17569 | 8286 | 1997 | 6.6 | 32459 | 18961 | 8870 | 2034 | 6.6 | 32459 | 18961 | 8870 | 2034 |
|  | 4 | 162 | 11.77 | 22.3 | 125506 | 141083 | 42245 | 9953 | 22.3 | 125506 | 141083 | 42245 | 9953 | 22.3 | 125506 | 141083 | 42245 | 9953 |
|  | 5 | 155 | 11.19 | 13.3 | 11491 | 14327 | 5530 | 2855 | 13.5 | 11646 | 14425 | 5582 | 2855 | 13.5 | 11646 | 14425 | 5582 | 2855 |
|  | 6 | 164 | 11.41 | 19.0 | 12698 | 2641 | 5862 | 0 | 19.0 | 12698 | 2641 | 5862 | 0 | 26.8 | 13828 | 2876 | 6384 | 0 |
| F | 1 |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  |
|  | 2 | 191 | 15.56 | 16.8 | 1113 | 1422 | 229 | 176 | 25.5 | 3074 | 1422 | 299 | 176 | 25.5 | 3074 | 1422 | 299 | 176 |
|  | 3 | 190 | 14.83 | 5.5 | 3524 | 4668 | 983 | 273 | 6.4 | 3867 | 4668 | 1309 | 546 | 6.4 | 3867 | 4668 | 1309 | 546 |
|  | 4 | 190 | 16.25 | 18.0 | 24951 | 37766 | 7257 | 876 | 23.2 | 32657 | 49821 | 8731 | 1533 | 23.2 | 32657 | 49821 | 8731 | 1533 |
|  | 5 |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  |
|  | 6 |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  | 0.0 |  |  |  |  |

Table 3.3.6. Egg production of sole (numbers per day x $10^{-6}$ ) in the eastern English Channel (VIId) in 1991 and the corresponding mid-point (days after 1 January) of the survey.

| Year: 1991 |  |  | N.day ${ }^{-1} \times 10^{-6}$ |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Survey | Mid-point | Temp | stage-1 | stage-2 | stage-3 | stage-4 |
| A | 83 | 7.8 | 19072 | 13581 | 4234 | 3313 |
| B | 105 | 8.8 | 53018 | 51276 | 10190 | 4853 |
| C | 139 | 10.1 | 15029 | 14279 | 6457 | 2677 |
| D | 154 | 11.3 | 8042 | 8041 | 3218 | 1179 |

Table 3.3.7. Egg production of sole (numbers per day $\times 10^{-6}$ ) in the western English Channel (VIIe) in 1991 and the corresponding mid-point (days after 1 January) of the survey. The egg production in survey was raised by a factor 4.3 to take account for the production in the southern part which was left unsampled (see text).

| Year: 1991 |  |  | N.day ${ }^{-1} \times 10^{-6}$ |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Survey | Mid-point | Temp | stage-1 | stage-2 | stage-3 | stage-4 |
| A | 60 | 8.79 | 11904 | 13521 | 2404 | 1566 |
| B | 79 | 8.60 | 28473 | 42409 | 20015 | 8840 |
| C | 111 | 9.64 | 21595 | 19352 | 8801 | 8302 |

Table 3.4.1. Time, day number after 1 January, of the peak in the production of stage 1 eggs calculated from a parabolic regression fitted through the observed values of log daily egg production rates of stage 1 , stage 2 and stage $3+4$ according to the GLM model: $\mathrm{Y}=\mathrm{D}$ $+D^{2}+S+A+Y R+A . Y R$, with $D$ is the day number after 1 January, $S$ is the egg stage (1-3), A is the area \#1-\#8, and YR is the year (1-5).

|  | 1984 | 1988 | $\begin{gathered} \text { Year } \\ 1989 \end{gathered}$ | 1990 | 1991 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Area |  |  |  |  |  |
| \#1 | 144 | 135 | 124 | 105 | 134 |
| \#2 | 144 | 137 | 128 | 116 | 136 |
| \#3 | 152 | 146 | 134 | 122 | 145 |
| \#4 | 160 | 155 | 144 | 138 | 154 |
| \#5 | 153 | 133 | - | - | 132 |
| \#6 | 168 | 164 | - | - | 161 |
| \#7 | - | - | - | - | 114 |
| \#8 | - | - | - | - | 90 |

Table 3.4.2. Average temperatures by survey for the different standard areas (\#) \#1-\#6: 5-m depth; \#7: integrated; \#8: surface

| Survey | \#1 | \#2 | \#3 | \#4 | \#5 | \#6 | \#7 | \#8 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1984-A | 7.0 | 5.9 | - | - | 6.3 | 5.6 | 6.9 | - |
| 1984-B | 8.4 | 8.6 | 8.6 | 7.5 | 8.4 | 7.0 | 8.8 | - |
| 1984-C | 10.2 | 9.3 | 9.3 | 9.5 | 9.4 | 9.0 | 9.2 | - |
| 1984-D | 14.5 | 12.2 | 13.0 | 12.4 | 13.1 | 11.2 | 11.1 | - |
| 1984-E |  |  |  |  |  |  |  |  |
| 1988-A | 7.6 | 7.0 | 6.9 | - | - | - | - | - |
| 1988-B | 9.1 | 8.0 | 7.3 | 7.3 | 8.8 | 8.0 | - | - |
| 1988-C | 11.9 | 10.6 | 11.9 | 10.5 | 11.2 | 10.4 | - | - |
| 1988-D | 14.4 | 13.7 | 13.8 | 13.4 | 13.5 | 13.0 | - | - |
| 1988-E | 16.2 | 15.8 | 16.1 | 16.3 | 16.0 | 15.1 | - | - |
| 1989-A | 8.7 | 7.6 | 6.8 | - | - | - | - | - |
| 1989-B | 8.4 | 7.8 | 7.5 | 7.0 | - | - | - | - |
| 1989-C | 12.9 | 12.8 | 12.0 | 12.1 | 12.3 | - | - | - |
| 1989-D | 15.0 | 15.4 | 15.5 | 16.6 | - | - | - | - |
| 1989-E | 17.3 | 15.8 | 16.8 | 17.4 | - | - | - | - |
| 1990-A | 8.1 | 7.4 | 7.6 | - | - | - | - | - |
| 1990-B | 8.7 | 7.8 | 7.6 | 7.1 | - | - | - | - |
| 1990-C | 11.0 | 9.5 | 9.0 | 9.3 | 10.0 | - | - | - |
| 1990-D | 13.6 | 13.1 | 12.7 | 12.5 | 13.0 | - | - | - |
| 1990-E | 15.8 | 14.8 | 14.9 | 14.2 | 14.5 | - | - | - |
| 1990-F | 16.0 | 16.1 | 16.6 | 15.6 | 15.5 | - | - | - |
| 1991-A | 4.6 | 4.4 | - | - | 5.3 | 4.7 | 7.8 | 8.8 |
| 1991-B | 6.6 | 6.3 | 4.4 | - | 7.8 | 6.2 | 8.8 | 8.6 |
| 1991-C | 8.7 | 7.6 | 7.4 | 7.0 | 8.1 | 6.6 | 10.1 | 9.6 |
| 1991-D | 9.7 | 9.3 | 11.2 | 10.3 | 9.2 | 8.7 | 11.3 | - |
| 1991-E | 12.0 | 11.9 | 12.0 | 11.3 | 11.4 | 11.1 | - | - |
| 1991-F | - | 16.3 | 17.0 | 16.6 | - | - | - | - |

Table 3.4.3. Ambient temperature by standard area and survey year. The ambient temperature reflects the average temperature experienced by a sole egg, and is calculated as the weighted average over the production curve.of stage l eggs.

| Survey year | Standard area |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | \#1 | \#2 | \#3 | \#4 | \#5 | \#6 | \#7 | \#8 |
| 1984 | 10.5 | 8.8 | 9.6 | 10.6 | 9.5 | 10.2 | - | - |
| 1988 | 10.3 | 8.9 | 9.9 | 10.9 | 9.7 | 9.6 | - | - |
| 1989 | 9.5 | 8.5 | 9.0 | 8.6 | - | - | - | - |
| 1990 | 9.9 | 9.2 | 8.8 | 10.3 | - | - | - | - |
| 1991 | 9.4 | 9.6 | 10.8 | 11.2 | 9.4 | 9.9 | 9.4 | 9.0 |

Table 3.5.1. Estimated $\log _{\mathrm{n}}$ egg production by area and year, the extrapolated number of fertilized eggs and the instantaneous mortality coefficients (M) during the egg stage.

|  | developmental egg stage |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 1 | 2 | 3 | 4 | fertilized | M |
| Year 1984 |  |  |  |  |  |  |
| \#1 | 7.772 | 7.718 | 6.292 | 5.020 | 8.64 | 0.547 |
| \#2 | 7.217 | 7.816 | 6.353 | 5.261 | 8.16 | 0.337 |
| \#3 | 7.167 | 6.706 | 5.720 | 2.681 | 8.50 | 0.727 |
| \#4 | 8.384 | 7.814 | 6.635 | 4.527 | 9.40 | 0.728 |
| \#5 | 7.341 | 7.099 | 5.630 | 3.497 | 8.51 | 0.640 |
| \#6 | 7.509 | 6.871 | 5.797 | 4.453 | 8.19 | 0.546 |
| Year 1988 |  |  |  |  |  |  |
| \#1 | 7.042 | 7.216 | 5.176 | 4.160 | 8.03 | 0.607 |
| \#2 | 6.206 | 5.682 | 4.058 | 2.873 | 7.00 | 0.560 |
| \#3 | 6.025 | 6.482 | 4.242 | - | 7.09 | 0.610 |
| \#4 | 6.664 | 6.788 | 4.337 | 3.891 | 7.53 | 0.682 |
| \#5 | 7.259 | 7.226 | 5.886 | 4.158 | 8.28 | 0.551 |
| \#6 | 5.267 | 4.560 | 2.973 | 2.945 | 5.58 | 0.437 |
| Year 1989 |  |  |  |  |  |  |
| \#1 | 7.728 | 7.784 | 6.857 | 6.002 | 8.32 | 0.304 |
| \#2 | 7.242 | 6.894 | 5.934 | 5.257 | 7.69 | 0.295 |
| \#3 | 7.063 | 6.917 | 5.478 | 3.405 | 8.22 | 0.574 |
| \#4 | 8.039 | 7.795 | 6.527 | 4.847 | 8.98 | 0.477 |
| Year 1990 |  |  |  |  |  |  |
| \#1 | 8.492 | 8.615 | 7.634 | 6.444 | 9.24 | 0.375 |
| \#2 | 8.476 | 8.742 | 7.774 | 6.523 | 9.27 | 0.328 |
| \#3 | 8.674 | 8.892 | 7.568 | 5.232 | 9.97 | 0.529 |
| \#4 | 8.760 | 8.465 | 7.342 | 4.927 | 9.93 | 0.678 |
| Year 1991 |  |  |  |  |  |  |
| \#1 | 8.249 | 8.389 | 7.531 | 6.398 | 8.95 | 0.317 |
| \#2 | 8.464 | 8.395 | 7.241 | 6.273 | 9.14 | 0.385 |
| \#3 | 8.267 | 8.218 | 7.523 | 6.427 | 8.87 | 0.368 |
| \#4 | 9.327 | 9.345 | 7.705 | 6.417 | 10.28 | 0.638 |
| \#5 | 7.680 | 7.528 | 6.453 | 5.435 | 8.33 | 0.376 |
| \#6 | 7.114 | 6.475 | 6.044 | 3.406 | 8.11 | 0.592 |
| \#7 | 7.814 | 7.727 | 6.409 | 5.722 | 8.42 | 0.367 |
| \#8 | 7.487 | 7.650 | 6.782 | 6.326 | 7.93 | 0.213 |

Table 3.5.2. Estimated production of fertilzed eggs ( $\times 10^{-12}$ ) for different parts of the North Sea.

| Area | 1984 | 1988 | 1989 | 1990 | 1991 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| North Sea |  |  |  |  |  |
| \#1 | 5.7 | 3.1 | 4.1 | 10.3 | 7.7 |
| \#6 | 3.6 | 0.3 | - | - | 3.3 |
| sum \# 1,5 | 10.1 | 7.1 | - | - | 11.8 |
| sum \# 2,3,4 | 18.3 | 4.9 | 12.4 | 46.2 | 43.6 |
| sum \# 1-6 | 32.0 | 12.1 | - | - | 57.9 |
| sum \# 1-4 | 23.9 | 11.9 | 15.9 | 55.0 | 50.9 |
| Channel |  |  |  |  |  |
| \#7 | - | - | - | - | 4.56 |
| \#8 | - | - | - | - | 2.79 |

Table 4.2.2.1 Regression coefficients from the relationship between $\ln$ fecundity and In gutted weight for sole from 1 Vb west and V11d over the period 1988-1991.

|  | INTERCEPT |  | SLOPE |  |
| :---: | :---: | :---: | :---: | :---: |
|  | IVb | VId | IVb | VIId |
| Year |  |  |  |  |
| 1988 | 5.99 | 5.80 | 1.09 | 1.15 |
| 1989 | 3.24 | 6.01 | 1.51 | 1.12 |
| 1990 | 3.88 | 5.95 | 1.42 | 1.12 |
| 1991 | 4.83 | 5.24 | 1.27 | 1.23 |

Table 4.2.2.2 ANOVA table from regression of fecundity on gutted weight of sole.

| Source of variation | SS | dr | MS | F | Pr>F |
| :---: | :---: | :---: | :---: | :---: | :---: |
| In gutted wt | 116.762 | 1 | 116.762 | 1750.61 | 0.0001 |
| Area | 0.397 | 1 | 0.397 | 5.95 | 0.015 |
| Year | 0.450 | 3 | 0.150 | 2.25 | 0.083 |
| Error | 21.077 | 316 | 0.067 |  |  |
| Total | 151.470 | 331 |  |  |  |

Area SS derived from: RSS due to model of $\ln f e c=a(a r, y r)+b(y r) \ln g w t$

- RSS due to model of $\ln \mathrm{fec}=\mathrm{a}(\mathrm{ar}, \mathrm{yr})+\mathrm{b}(\mathrm{ar}+\mathrm{yr}) \ln (\ln \mathrm{gwt})$

Year SS derived from: RSS due to model of $\ln \mathrm{fec}=\mathrm{a}(\mathrm{ar}, \mathrm{yr})+\mathrm{b}(\mathrm{ar}) \ln \mathrm{gwt}$

- RSS due to model of $\ln \mathrm{fec}=\mathrm{a}(\mathrm{ar}, \mathrm{yr})=\mathrm{b}(\mathrm{ar}+\mathrm{yr}) \ln \mathrm{gwt}$
where $\ln \mathrm{fec}=\ln$ fecundity, $\ln \mathrm{gwt}=\ln$ gutted weight, ar=area, $\mathrm{yr}=\mathrm{year}$

Table 4.3.1. Prevalence and relative intensity of atresia in fecundity samples of prespawning females collected for the 1991 sole fecundity survey in ICES areas IV, VII and VIII. Prevalence is defined as the proportion of fish in the sample showing any atresia. Intensity is defined the number of alpha atretic oocytes in a fishes ovaries expressed as the log transformed mean of atresia intensity / predicted fecundity at length restricted to fish with atresia.

| Area | Prevalence | Relative intensity | Number of fish |
| :---: | :---: | :---: | :---: |
| IVb (cast) | 0.175 | 0.017 | 40 |
| IVb (west) | 0.044 | 0.023 | 45 |
| IVc | 0.182 | 0.025 | 55 |
| VIIa | 0.690 | 0.076 | 29 |
| VIId | 0.082 | 0.028 | 49 |
| VIIe | 0.061 | 0.017 | 33 |
| VIII | 0.152. | 0.026 | 33 |
| Progress in spawning (sample IVb east) |  |  |  |
| <0.50 | 0.40 | 0.038 | 15 |
| 0.50-0.75 | 0.40 | 0.045 | 68 |
| 0.75-1.00 | 0.46 | 0.018 | 60 |

Table 4.5.1. Mean egg size, standard deviation (S.D), number of observations (n), daily egg production and mid-points, for cruises C, D and E of the 1991 sole egg survey in stations off the Belgian coast and in the inner German Bight. An overall seasonal average egg size and egg volume was calculated from the average egg-size and egg-volume per cruise weighted over the production values.

| Cruise | Mid-point day-1 | Production | stage 1 | stage 2 | stage 3 | stage 4 | total |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Belgium coast |  |  |  |  |  |  |  |
| mean | 106 | 52607 | 1.217 | 1.222 | 1.226 | 1.238 | 1.223 |
| S.D. |  |  | 0.054 | 0.048 | 0.049 | 0.049 | 0.05 |
| n |  |  | 110 | 110 | 110 | 24 | 354 |
| mean | 135 | 58739 | 1.217 | 1.207 | 1.226 | 1.235 | 1.218 |
| S.D. |  |  | 0.054 | 0.056 | 0.05 | 0.057 | 0.055 |
| n |  |  | 131 | 104 | 76 | 32 | 343 |
| mean | 162 | 13327 | 1.141 | 1.128 | 1.129 | 1.2 | 1.136 |
| S.D. |  |  | 0.078 | 0.037 | 0.057 |  | 0.066 |
| n |  |  | 32 | 12 | 14 | 1 | 59 |
|  |  | mean | 1.2089 | 1.2049 | 1.2156 | 1.2325 | 1.2113 |
| German Bight |  |  |  |  |  |  |  |
| mean | 113 | 67961 | 1.193 | 1.230 | 1.300 |  | 1.204 |
| S.D. |  |  | 0.057 | 0.050 | 0.027 |  | 0.058 |
| n |  |  | 136 | 44 | 4 |  | 184 |
| mean | 150 | 361076 | 1.074 | 1.075 | 1.082 | 1.079 | 1.077 |
| S.D. |  |  | 0.054 | 0.069 | 0.051 | 0.035 | 0.056 |
| n |  |  | 127 | 78 | 106 | 8 | 319 |
| mean | 167 | 157965 | 1.087 | 1.099 | 1.099 | 1.124 | 1.097 |
| S.D. |  |  | 0.045 | 0.044 | 0.045 | 0.041 | 0.046 |
| n |  |  | 196 | 127 | 138 | 49 | 510 |
|  |  | mean | 1.091 | 1.099 | 1.112 | 1.093 | 1.083 |

Table 5.1.1. Sexes combined VPA. Stock numbers of males and females, and the average proportion of females (1985-89), second quarter weight (1982-1991) and percentage maturity (1982-1991).

|  | Stock numbers at 1 April |  |  |  |  | sex ratio | weight | \%mat |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 1984 | 1988 | 1989 | 1990 | 1991 |  |  |  |
| 1 | 70425 | 327888 | 119020 | 128298 | 68423 | 0.50 | 0.025 | 0.00 |
| 2 | 130383 | 60388 | 296685 | 107479 | 115049 | 0.50 | 0.139 | 0.05 |
| 3 | 90404 | 101980 | 42130 | 223782 | 78988 | 0.50 | 0.220 | 0.66 |
| 4 | 47361 | 30567 | 47697 | 20891 | 102686 | 0.50 | 0.333 | 0.96 |
| 5 | 20392 | 10014 | 13247 | 21806 | 9676 | 0.51 | 0.429 | 1.00 |
| 6 | 1828 | 10932 | 4898 | 7534 | 10893 | 0.51 | 0.491 | 1.00 |
| 7 | 2103 | 4545 | 6207 | 2827 | 3212 | 0.51 | 0.543 | 1.00 |
| 8 | 3431 | 2500 | 2640 | 4236 | 1459 | 0.51 | 0.613 | 1.00 |
| 9 | 1692 | 1958 | 1412 | 1768 | 2629 | 0.52 | 0.673 | 1.00 |
| 10 | 858 | 360 | 1273 | 835 | 1029 | 0.54 | 0.679 | 1.00 |
| 11 | 795 | 168 | 290 | 924 | 502 | 0.55 | 0.795 | 1.00 |
| 12 | 531 | 376 | 119 | 220 | 530 | 0.58 | 0.765 | 1.00 |
| 13 | 154 | 173 | 259 | 74 | 143 | 0.61 | 0.806 | 1.00 |
| 14 | 89 | 43 | 116 | 190 | 41 | 0.65 | 0.824 | 1.00 |
| 15 | 915 | 524 | 407 | 647 | 494 | 0.70 | 0.871 | 1.00 |

Table 5.1.2. Spawning stock biomass of female North Sea sole by age-group calculated from the stock numbers of males and females, and the average proportion of females (1985-89), second quarter weight (1982-1991) and percentage maturity (1982-1991) from Table 5.1.1.

|  | 1984 | 1988 | 1989 | 1990 | 1991 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | 0 | 0 | 0 | 0 | 0 |
| 2 | 453 | 210 | 1031 | 373 | 400 |
| 3 | 6563 | 7404 | 3059 | 16247 | 5735 |
| 4 | 7570 | 4886 | 7624 | 3339 | 16413 |
| 5 | 4462 | 2191 | 2898 | 4771 | 2117 |
| 6 | 458 | 2737 | 1227 | 1887 | 2728 |
| 7 | 582 | 1259 | 1719 | 783 | 889 |
| 8 | 1073 | 782 | 825 | 1324 | 456 |
| 9 | 592 | 685 | 494 | 619 | 920 |
| 10 | 315 | 132 | 467 | 306 | 377 |
| 11 | 348 | 73 | 127 | 404 | 219 |
| 12 | 236 | 167 | 53 | 98 | 235 |
| 13 | 76 | 85 | 127 | 36 | 70 |
| 14 | 48 | 23 | 62 | 102 | 22 |
| 15 | 558 | 319 | 248 | 394 | 301 |
| Total |  |  |  |  |  |
| SSB | 23332 | 20953 | 19961 | 30683 | 30883 |

Table 5.1.3. Estimate of female spawning stock biomass for VIId sole in 1991.

| Age | Stock numbers 1-1-1991 (thousands) | Z-q1 | Stock numbers 1-4-1991 (thousands) | Sex-ratio | Maturity | Weight Q2 <br> (kg) | SSB female (tonnes) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | 16873 | 0.025 | 16452 | 0.5 | 0.00 | 0.063 | 0 |
| 2 | 16099 | 0.097 | 14607 | 0.5 | 0.07 | 0.124 | 63 |
| 3 | 9332 | 0.213 | 7544 | 0.7 | 0.97 | 0.182 | 932 |
| 4 | 5255 | 0.190 | 4346 | 0.7 | 1.00 | 0.237 | 721 |
| 5 | 1255 | 0.160 | 1069 | 0.7 | 1.00 | 0.289 | 216 |
| 6 | 2140 | 0.193 | 1764 | 0.7 | 1.00 | 0.340 | 420 |
| 7 | 320 | 0.160 | 273 | 0.7 | 1.00 | 0.387 | 74 |
| 8 | 563 | 0.172 | 474 | 0.7 | 1.00 | 0.432 | 143 |
| 9 | 338 | 0.143 | 293 | 0.7 | 1.00 | 0.474 | 97 |
| 10+ | 1283 | 0.143 | 1113 | 0.7 | 1.00 | 0.546 | 425 |

Table 5.1.4. Estimate of female spawning stock biomass for VIId sole in 1991.

| Age | Stock numbers 1-1-1991 (thousands) | Z-ql | Stock numbers 1-4-1991 (thousands) | Sex-ratio | Maturity | $\begin{aligned} & \text { Weight } \\ & \text { Q2 } \\ & (\mathrm{kg}) \end{aligned}$ | SSB female (tonnes) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | 5565 | . 025 | 5426 | 0.50 | 0.00 | 0.076 | 0 |
| 2 | 5413 | . 040 | 5202 | 0.54 | 0.07 | 0.143 | 28 |
| 3 | 2235 | . 116 | 1991 | 0.69 | 0.61 | 0.206 | 173 |
| 4 | 1607 | . 152 | 1380 | 0.71 | 0.77 | 0.266 | 201 |
| 5 | 659 | . 164 | 559 | 0.80 | 1.00 | 0.322 | 144 |
| 6 | 583 | . 134 | 510 | 0.71 | 1.00 | 0.376 | 136 |
| 7 | 330 | . 107 | 297 | 0.82 | 1.00 | 0.426 | 104 |
| 8 | 517 | . 201 | 423 | 0.85 | 1.00 | 0.473 | 170 |
| 9 | 112 | . 139 | 97 | 0.84 | 1.00 | 0.518 | 42 |
| 10+ | 700 | . 139 | 609 | 0.87 | 1.00 | 0.650 | 344 |
| Total |  |  |  |  |  |  | 1342 |

Figure 3.1. Standard areas distinguished to calculate the production of fertilized eggs in the North Sea (area \#1-\#6), the eastern (\#7) and western English Channel (\#8). Notify that the western English Channel is only partly shown





Figure 3.2.1. Distribution of stage 1 eggs of North Sea Sole in 1984


NORTH SEA SURVEY 3 - 24th MAY 1988



NORTH SEA SURVEY 4 - 24th JUNE 1988


NORTH SEA SURVEY 5 - 23rd JULY 1938


Figure 3.2.2. Distribution of stage 1 eggs of North Sea sole in 1988.


NORTH SEA SURVEY 3 - 29th MAY 1989



NORTH SEA SURVEY 4 - 23rd JUNE 1989


NORTH SEA SURVEY 5 - 13th JULY 1989


Figure 3.2.3. Distribution of stage 1 eggs of North Sea sole in 1989.

NORTH SEA SURVEY 1 - 13 th MARCH 1990


NORTH SEA SURVEY $3-28$ th APRIL 1990



NORTH SEA SURVEY 4 - 28th MAY 1990



Figure 3.2.4. Distribution of stage 1 eggs of North Sea sole in 1990.

NORTH SEA SURVEY 2 - 20th MARCH 1991


NORTH SEA SURVEY 4 - 16th MAY 1991


NORTH SEA SURVEY 3 - 20th APRIL 1991


NORTH SEA SURVEY 5-12th JUNE 1991


NORTH SEA SURVEY 6 - 10th JULY 1991


Figure 3.2.5. Distribution of stage 1 eggs of North Sea sole in 1991.


## EASTERN CHANNEL SURVEY 3 - 23rd MAY 1984




EASTERN CHANNEL SURVEY 4 - 18th JUNE 1984


Figure 3.2.6. Distribution of stage 1 eggs of sole in the eastern English Channel (VIId) in 1984.



EASTERN CHANNEL SURVEY 3 - 19th MAY 1391


EASTERN CHANNEL SURVEY 4 - 3rd JUNE 1991




Figure 3.2.8. Distribution of stage 1 eggs of sole in the western English Channel (Vחe) in 1991

WESTERN CHANNEL SURVEY 1 - 1 st MARCH 1991
WESTERN CHANNEL SURVEY 2-20th MARCH 1991


WESTERN CHANNEL SURVEY 3-21ST APRIL 1991
$\bullet$



Figure 3.4.1. Production curve (N.day-1) of sole eggs in 1984 in the standard areas \#1 - \#6 of the North Sea



Figure 3.4.2. Production curve (N.day-1) of sole eggs in 1988 in the standard areas \#1-\#6 of the North Sea



1989 AREA3


Figure 3.4.1. Production curve (N.day-1) of sole eggs in 1989 in the standard areas \#1 - \#4 of the North Sea



1990 AREA3


1990 AREA4


Figure 3.4.4. Production curve (N.day-1) of sole eggs in 1990 in the standard areas \#1 - \#6 of the North Sea



Figure 3.4.5. Production curve (N.day-1) of sole eggs in 1991 in the standard areas \#1-\#6 of the North Sea



Figure 3.4.6. Production curve (N.day-1) of sole eggs in 1991 in the eastern English Channel (\#7) and western English Channel (\#8)


Figure 3.4.7. Parabolic regressions through the logn daily egg production of stage 1 against time (days after 1 January) in the standard areas (\#1-\#6) in the North Sea in 1991.


Figure 3.4.8. Annual and geographical differences in the time of peak spawning (day after 1 January)


Figure 3.4.9. Spring increase in water temperature and the timing of the peak of spawning in 1991 in the North Sea (areas \#1-\#6) and western English Channel (VIIe).


Figure 3.4.10 Differences in the increase in sea temperature illustrated by the average monthly temperature at a station in the entrance of the western Wadden Sea (den Helder)








Figure 3.5.1. Plots of the $\log _{\mathrm{n}}$ Egg production against mean age of stage 1, 2, 3 and 4 eggs for different years in the North Sea (\#1-\#6), eastern (\#7) and western (\#8) English Channel. The regression lines indicate the extrapolation to the number of fertilized eggs at $t=0$.


Figure 4.1. Map with locations and dates of fecundity samples collected in 1991.

Figure 4.1.1. Plots and statistics of the fecundity - body size relationships in the eight sampling areas in 1991. Model: $\mathrm{Y}=$ constant $\mathrm{X}^{\text {coefficient }}$



Regression Ouṭut:
Constant
Std Err of Y Est
R Squared
No. of Observations
Degrees of Freedom

X Coefficient(s)
Std Err of Coef.

Regression Output:

| Constant | -0.29856 |
| :--- | ---: |
| Std Er of Y Est | 0.20172 |
| R Squared | 0.805726 |
| No. of Observations | 40 |
| Degrees of Freedom | 38 |


| X Coefficient(s) | 3.740706 |
| :--- | :--- |
| Std Er of Coef. | 0.205934 |




Regression Output:

| Constant | -0.56167 |
| :--- | ---: |
| Std ErT of Y Est | 0.246092 |
| R Squared | 0.878738 |
| No. of Observations | 55 |
| Degrees of Freedom | 53 |


| X Coefficient(s) | 3.806479 |
| :--- | :--- |
| Std Err of Coef. | 0.194231 |

$\begin{array}{ll} & \\ X \text { Coefficient(s) } & 4.169849 \\ \text { Sid Er of Coef. } & 0.343184\end{array}$

Figure 4.1.1. continued.


Fecundity $v$ length


Regression Cutput:

| Constant | 0.598738 |  |
| :--- | ---: | ---: |
| Sid Er of Y Est | 0.259069 |  |
| R Squared | 0.741361 |  |
| No. of Observations | 33 |  |
| Degrees of Freedom | 31 |  |
| $\quad$ R= |  | 0.861023 |
| X Coefficient(s) | 3.336464 |  |
| Sid Er of Coef. | 0.353946 |  |

Fecundity $v$ length
Sole Area VIII (Biscay) 1991


Regression Outut

| Constant | -252197 |
| :--- | ---: |
| Sid Er of Y Est | 0.218238 |
| R Squared | 0.879268 |
| No. of Observations | 39 |
| Degrees of Freeciom | 37 |

Figure 4.1.2. Plots and statistics of the fecundity - body weight relationships in the eight sampling areas in 1991. Model: $\mathrm{Y}=$ constant X coefficient



Regression Output:

| Regression Oupur: |  |
| :--- | ---: |
| Constant | -655028 |
| Std Err of Y Est | 63958.25 |
| R Squared | 0.872772 |
| No. of Observations | 45 |
| Degrees of Freedom | 43 |
|  |  |
| X Coefficient(s) | 838.3259 |
| Std Er of Coef. | 48.81112 |

Regression Output:

| Constant | -42840.2 |
| :--- | ---: |
| Std Err of Y Est | 102235.6 |
| R Squared | 0.913019 |
| No. of Observations | 40 |
| Degrees of Freedom | 38 |
|  |  |
| X Coefficient(s) | 1097.092 |
| Std Er of Coef. | 54.93162 |

Fecundity $v$ gutted weisit
sole area IVC 198i


Regression Outurt:

| Constant | -23624.7 |
| :--- | ---: |
| Std Er of Y Est | 10152.4 |
| Q Squared | 0.890662 |
| No. of Observations | 55 |
| Degrees of Freedom | 53 |

Fecundity $v$ Weicht Sole area VIID 1991


Regression Cuṭut:
Consiant
$-64831.4$
99789.07
0.766266

49
47

Figure 4.1.2. comtinued.

Fecundity v Gu:Eed weignt


Regression Cutur:

| Constant | -15518.9 |
| :--- | ---: |
| Sid Er of Y Est | 110603.4 |
| R Squared | 0.74504 |
| No. of Observations | 33 |
| Degrees of Freedom | 31 |
| $=$ | 0.86350 .4 |
| X Coefficient(s) | 685.2224 |
| Std Err of Coef. | 71.88048 |



Regression Cutur:

| Constant | -10964.6 |
| :--- | ---: |
| Std Er of Y Es: | 65131.27 |
| R Squared | 0.56594 |
| No. of Cbservatons | $\approx 9$ |
| Degrees of Freedom | 37 |

$\times$ Ccerficentis:
673.205

Sid Err cl Coet. 43.3453

Regression Outut:
Consiant
Std Err of Y Est
R Squared
No. of Cbservations
Degrees of Freecom
X Coerficientis) $\quad 64.5 .9006$
Std Er of Coef. $\quad 55.1476$

Figure 4.1.3. Fecundity - length and fecundity -body weight relationships and predicted fecundities for the pooled data of the areas which did not show a significant different relationship. Data for 1991.


|  | Predicted fecundity | Regression of Loge transformed data Years 88-91 combined |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| AREA | at 37 cm | slope | constant |  | Slope | constant |
| IVB (east) \& IVC | 545370 | 4.014 | -1.285 |  |  |  |
| VIIA \& VIID | 414663 | 4.014 | -1.559 | VIID only | 4.25 | -2.373 |
| IVB (west) | 324234 | 4.014 | -1.805 |  | 4.25 | -2.578 |
| VIIE, VIII, \& IX | 273818 | 4.014 | -1.974 |  |  |  |



Regression data

AREA
IVB (east) \& IVC
VIIA \& VIID
IVB (west)
VIIE, VIII, \& IX

|  |  |
| :---: | :---: |
| slope | constant |
| 1084 | -30068 |
| 975.5 | -61527 |
| 838.3 | 69503 |
| 626.1 | -17683 |

Years 88-91 combined Slope constant $1176 \quad 5619$
$\begin{array}{lll}\text { VIID only } & 1.176 & 5.619 \\ & 1.323 & 4.495\end{array}$ loge transformed dat

Figure 4.1.4. Annual differences in the fecundity - body size relationship in the western


Figure 4.1 5. Annual differences in the fecundity - body size relationship in the eastern English Channel (VIId)


Figure 4.2.1. Frequency distributions of oocytes in the range of $150-450 \mu \mathrm{~m}$ of female sole which contained $95 \%-55 \%$ of their prespawning stock of vitellogenic oocytes.











Figure 4.2.2. Frequency distributions of oocytes in the range of $150-450 \mu \mathrm{~m}$ of female sole which contained $30 \%$ of their prespawning stock of vitellogenic oocytes.





Regression Output:

| Constant | 4.59959 |  |  |  |
| :--- | ---: | ---: | ---: | ---: |
| Std Err of Y Est | 0.59505 |  |  |  |
| R Squared | 0.019237 | R $=$ | 0.138698 |  |
| No. of Observations | 38 |  |  |  |
| Degrees of Freedom | 36 |  |  |  |
|  |  |  |  |  |
| X Coefficient(s) | 1.239668 |  |  |  |
| Std Err of Coef. | 1.475246 |  |  |  |
|  |  |  |  |  |
| log transformed data |  |  |  |  |

Figure 4.2.3. Batch fecundity of sole in IVB (east) collected at $15 / 5$ and 27/5-16/6 1991.

Size frequency of atretic ooctye profiles seen in histological section

4.3.1. Size frequency distribution of atretic oocyte profile seen in histological section.


Figure 4.4.1. Frequency of maturity stages of female sole by month in the Southern Bight (above) and German Bight (below). Maturity stage 5-6 represents spawning females of age group $5+$. Data: Dutch market sampling
programme 1970-1979.


Figure 4.4.2. Cumulative frequency of maturity stages of female sole by month in the Southern Bight (above) and German Bight (below). Data of age group $5+$ females from Dutch market sampling programme 1970-1979.


Figure 4.4.3. Cumulative frequency of maturity stages of female sole by 10 -days period after 1 March in the Southern Bight (above) and German Bight (below). Data of age group $5+$ females from Dutch market sampling programme 1970-1979.


Figure 4.5.1. Mean egg size and its standard deviation against time of the year (days after 1 January) of sole eggs collected in the inner German Bight, along the Belgian coast and on the UK coast of VIId during the egg surveys between 1988 and 1991.


Figure 6.1. Scatter plot of the SSB estimate (1000 t) obtained by VPA and egg surveys (present study and Horwood, 1992)


[^0]:    * General Secretary

    ICES
    Palægade 2-4
    DK-1261 Copenhagen K
    DENMARK
    https://doi.org/10.17895/ices.pub. 9281

