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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 µm 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 cm diameter nose cone and 420 µm 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 1m 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-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 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 µm in survey A and 500 µm in survey C. During survey B a modified Gulf III sampler with a 500 µm 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-m above the sea bed, filtering at least 50 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-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 (N_i) of stage i were calculated per m^2 and converted into a number per m^2 per day using the developmental time (d_i) calculated according to the formulae given by Anon (1986) (Table 3.1.2.). For each area j the production (P_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 N_i values of surrounding stations. If a larger area was not sampled the observed $_aP_i$ 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 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.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°30' N, where the distance between the English and continental coast becomes smaller, spawning takes place all over the area. North of 52°30' 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 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 (mid-date 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 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 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 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 $m^{-2}.day^{-1}$ 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 (#)	extrapolation from
1984	A	2	1984 B2
1984	A	6	1984 B6
1984	C	2	1984 B2
1984	D	1	1984 C1
1984	D	5	1984 C5
1984	D	6	1984 C6
1988	D	1	zeros
1988	D	3	zeros
1989	A	2	1989 B2
1989	A	3	1989 B3
1989	E	2	zeros
1990	A	2	1990 B2
1990	A	3	1990 B3
1991	A	1	zeros
1991	A	2	zeros
1991	A	5	zeros

1991	A	6	zeros
1991	B	6	zeros
1991	C	6	1984 B6
1991	D	3	1991 E3
1991	D	4	1991 E4
1991	D	6	1984 C6
1991	E	6	1984 D6

The production estimates for each survey including the surface areas sampled (10^{-3} 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-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 egg-production 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 dY/dt = 0. Thus, given the parabole - $\log_n N = a + b\,t + c\,t^2$ - the peak in egg production (t_{max}) can be calculated as t_{max} = b/2c. 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:

$$Y = a + (b_{common} + b_{area} + b_{year})\,t + (c_{common} + c_{area} + c_{year})\,t^2 +$$

$$\text{STAGE} + \text{AREA} + \text{YEAR} + \text{AREA.YEAR} + \text{STAGE.AREA.YEAR.}$$

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 ($F_{54,191}$=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 ($F_{16,245}$=3.88; 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 °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 t_{max}- 60 and 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 $\log_n$ 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 µm in a refrigerated cabinet (-4°) 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 = $\alpha+\beta \ln L$		Fecundity = αW^{β}	
	α	β	α	β
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 = $\alpha + \beta \ln W$	
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 Pr>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 (Pr>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 6-12h. 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 VIIa 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 over-extended. 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 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 turnover 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: P x I x T, with P = prevalence, I = mean intensity (log transformed x duration of the spawning stage) and 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 from 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 x (F+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 ($x10^{-12}$) from egg surveys					
North Sea					
#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

italics indicate only partial sampling of the North Sea

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 egg .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 fishery-independent 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.

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

Survey	Sub-areas (#)	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					
A	#7	20-27/3	55	84	UK
B	#7	12-18/4	59	109	
C	#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 (T in °C) according the model: $D = \exp(\beta.T + \alpha)$. Modified from Riley (1974) according Anon (1986).

	α	β
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).

year:1984

		midday	Temp	sampled surface area					*including extrapolation rectangles*					including extrapolation areas				
survey	area	number	5-mtr	surface	stage I	stage II	stage III	stage IV	*surface*	*stage I*	*stage II*	*stage III*	*stage IV*	surface	**stage I**	**stage II**	**stage III**	**stage IV**
A	1	90.8	11.2	13.1	5678	250	0	0	*13.8*	*5678*	*250*	*0*	*0*	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	2.4	5410	3996	385	0	*2.4*	*5410*	*3996*	*385*	*0*	14.2	16477	12170	1173	0
	2	171	12.1	3.7*	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	11.1	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 x 10-6) in the North Sea in 1988 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).

		midday	Temp	sampled surface area					*including extrapolation rectangles*					including extrapolation areas				
survey	area	number	5-mtr	surface	stage I	stage II	stage III	stage IV	*surface*	*stage I*	*stage II*	*stage III*	*stage IV*	surface	stage I	stage II	stage III	stage IV
A	1	101	7.8	13.1	3568	2015	306	0	*13.6*	*3894*	*2105*	*306*	*0*	13.6	3894	2105	306	0
	2	96	7.0	18.5	2818	938	0	0	*25.9*	*2818*	*938*	*0*	*0*	25.9	2818	938	0	0
	3	96	6.9	1.8	671	0	0	0	*1.8*	*671*	*0*	*0*	*0*	1.8	671	0	0	0
	4			0.0					*0.0*					0.0				
	5			0.0					*0.0*					0.0				
	6			0.0					*0.0*					0.0				
B	1	124	9.3	12.8	16244	26982	4686	2268	*14.5*	*17577*	*27453*	*4735*	*2268*	14.5	17577	27453	4735	2268
	2	118	8.0	26.1	11463	5357	769	0	*26.1*	*11463*	*5357*	*769*	*0*	26.1	11463	5357	769	0
	3	116	7.4	6.4	6836	1748	0	0	*6.4*	*6836*	*1748*	*0*	*0*	6.4	6836	1748	0	0
	4	117	7.1	22.9	6666	161	0	0	*23.2*	*6666*	*161*	*0*	*0*	23.2	6666	161	0	0
	5	124	8.9	13.4	21256	29550	7422	522	*13.4*	*21256*	*29550*	*7422*	*522*	13.4	21256	29550	7422	522
	6	123	8.1	26.1	2906	192	0	0	*26.1*	*2906*	*192*	*0*	*0*	26.1	2906	192	0	0
C	1	145	12.2	13.8	22046	25866	2379	515	*14.2*	*24219*	*25866*	*2379*	*515*	14.2	24219	25866	2379	515
	2	144	12.0	25.9	5762	5368	1448	648	*26.0*	*6018*	*5368*	*1448*	*648*	26.0	6018	5368	1448	648
	3	151	11.9	6.7	7274	18607	2000	0	*7.0*	*7748*	*20860*	*2399*	*0*	7.0	7748	20860	2399	0
	4	142	11.8	23.3	19706	28810	2584	1750	*23.3*	*19706*	*28810*	*2584*	*1750*	23.3	19706	28810	2584	1750
	5	146	10.8	13.4	22410	9740	2369	1587	*13.4*	*22410*	*9740*	*2369*	*1587*	13.4	22410	9740	2369	1587
	6	145	10.3	26.1	5184	2360	539	680	*26.1*	*5184*	*2360*	*539*	*680*	26.1	5184	2360	539	680
D	1	179		11.8	0	0	0	0	*13.3*	*0*	*0*	*0*	*0*	14.2	0	0	0	0
	2	173		24.4	0	0	0	0	*25.5*	*0*	*0*	*0*	*0*	25.5	0	0	0	0
	3	174		5.7	0	0	0	0	*5.7*	*0*	*0*	*0*	*0*	6.9	0	0	0	0
	4	173	14.1	23.2	1873	2294	143	0	*23.2*	*1873*	*2294*	*143*	*0*	23.2	1873	2294	143	0
	5	180		12.3	0	0	0	0	*12.3*	*0*	*0*	*0*	*0*	12.3	0	0	0	0
	6	179	14.3	26.1	0	0	144	0	*26.1*	*0*	*0*	*144*	*0*	26.1	0	0	144	0
E	1	207		14.2	0	0	0	0	*14.2*	*0*	*0*	*0*	*0*	14.2	0	0	0	0
	2	203		25.4	0	0	0	0	*25.4*	*0*	*0*	*0*	*0*	25.4	0	0	0	0
	3	200		5.5	0	0	0	0	*5.5*	*0*	*0*	*0*	*0*	6.9	0	0	0	0
	4	201	16.8	22.3	739	481	0	0	*22.3*	*739*	*481*	*0*	*0*	22.3	739	481	0	0
	5	207	16.3	9.0	0	0	1521	0	*12.3*	*0*	*0*	*3042*	*0*	12.3	0	0	3042	0
	6	208	14.5	26.1	0	1016	0	0	*26.1*	*0*	*1016*	*0*	*0*	26.1	0	1016	0	0

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-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).

		midday	Temp	sampled surface area					*including extrapolation rectangles*					**including extrapolation areas**				
survey	area	number	5-mtr	surface	stage I	stage II	stage III	stage IV	*surface*	*stage I*	*stage II*	*stage III*	*stage IV*	surface	**stage I**	**stage II**	**stage III**	**stage IV**
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 x 10-6) in the North Sea in 1990 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: 1990

				sampled surface area					*including extrapolation rectangles*					**including extrapolation areas**				
survey	area	midday number	Temp 5-mtr	surface	stage I	stage II	stage III	stage IV	*surface*	*stage I*	*stage II*	*stage III*	*stage IV*	surface	**stage I**	**stage II**	**stage III**	**stage IV**
A	1	72	8.50	13.9	27663	16163	3819	0	*13.9*	*27663*	*16163*	*3819*	*0*	13.9	27663	16163	3819	0
	2	72	7.40	14.2	26159	9882	2198	1166	*14.2*	*26159*	*9882*	*2198*	*1166*	25.5	29037	10969	2440	1294
	3	73	7.60	4.8	10035	7326	1629	0	*4.8*	*10035*	*7326*	*1629*	*0*	6.7	15875	11590	2577	0
	4			0.0					*0.0*					0.0				
	5			0.0					*0.0*					0.0				
	6			0.0					*0.0*					0.0				
B	1	86	8.70	13.3	85837	87680	31604	8782	*13.9*	*85837*	*87680*	*31604*	*8782*	13.9	85837	87680	31604	8782
	2	88	8.10	23.5	50826	65536	21453	8115	*25.9*	*58076*	*68943*	*24033*	*9156*	25.9	58076	68943	24033	9156
	3	88	7.60	5.9	85361	77472	29780	2773	*6.7*	*106600*	*88782*	*34784*	*3742*	6.7	106600	88782	34784	3742
	4	87	7.10	0.9	184	8122	2213	1155	*0.9*	*184*	*8122*	*2213*	*1155*	0.9	184	8122	2213	1155 *
	5			0.0					*0.0*					0.0				
	6			0.0					*0.0*					0.0				
C	1	116	9.30	14.1	59788	77895	35852	10501	*14.1*	*59788*	*77895*	*35852*	*10501*	14.1	59788	77895	35852	10501
	2	116	9.10	21.7	83760	124448	47982	13180	*25.3*	*83760*	*124448*	*47982*	*13180*	25.3	83760	124448	47982	13180
	3	122	10.20	6.4	66695	125980	23505	1772	*6.4*	*66695*	*125980*	*23505*	*1772*	6.4	66695	125980	23505	1772
	4	122	11.30	15.1	141591	70040	19485	1094	*22.0*	*148456*	*72367*	*20220*	*1060*	22.0	153207	74683	20867	1094
	5	123	10.30	9.9	18971	47637	19753	3635	*9.9*	*18971*	*47637*	*19753*	*3635*	9.9	18971	47637	19753	3635 *
	6			0.0					*0.0*					0.0				
D	1	142	13.70	14.1	17491	28610	6842	3351	*14.1*	*17491*	*28610*	*6842*	*3351*	14.1	17491	28610	6842	3351
	2	151	13.20	21.8	13578	21848	9811	1175	*25.5*	*13578*	*21848*	*10093*	*1385*	25.5	13578	21848	10093	1385
	3	149	12.70	6.4	47685	44166	14253	1275	*6.4*	*47685*	*44166*	*14253*	*1275*	6.4	47685	44166	14253	1275
	4	142	12.60	22.1	55908	63504	21967	2646	*22.4*	*58892*	*65724*	*22542*	*2646*	22.4	58892	65724	22542	2646
	5	153	12.70	3.0	614	7287	0	0	*3.0*	*614*	*7287*	*0*	*0*	3.0	614	7287	0	0 *
	6			0.0					*0.0*					0.0				
E	1	177	16.10	14.2	711	991	13	825	*14.2*	*711*	*991*	*13*	*825*	14.2	711	991	13	825
	2	174	15.00	20.0	1022	0	0	0	*25.5*	*1022*	*0*	*0*	*0*	25.5	1022	0	0	0
	3	171	14.50	6.8	1428	6063	2038	742	*6.8*	*1428*	*6063*	*2038*	*742*	6.8	1428	6063	2038	742
	4	171	14.30	23.2	15135	29642	10820	1087	*23.2*	*15135*	*29642*	*10820*	*1087*	23.2	15135	29642	10820	1087
	5	178		2.9	0	0	0	0	*2.9*	*0*	*0*	*0*	*0*	2.9	0	0	0	0 *
	6			0.0					*0.0*					0.0				
F	1	192	16.10	14.2	1149	0	427	0	*14.2*	*1149*	*0*	*427*	*0*	14.2	1149	0	427	0
	2	197		15.4	0	0	0	0	*25.5*	*0*	*0*	*0*	*0*	25.5	0	0	0	0
	3	199	16.60	6.4	908	3465	326	0	*6.4*	*908*	*3465*	*326*	*0*	6.4	908	3465	326	0
	4	200	15.80	22.3	6353	1204	2252	221	*22.3*	*6353*	*1204*	*2252*	*221*	22.3	6353	1204	2252	221
	5	193		1.9	0	0	0	0	*1.9*	*0*	*0*	*0*	*0*	1.9	0	0	0	0 *
	6			0.0					*0.0*					0.0				

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

		midday	Temp	sampled surface area					*including extrapolation rectangles*					including extrapolation areas				
survey	area	number	5-mtr	surface	stage I	stage II	stage III	stage IV	*surface*	*stage I*	*stage II*	*stage III*	*stage IV*	surface	stage I	stage II	stage III	stage IV
A	1	50	4.36	13.4	0	0	0	0	*13.4*	*0*	*0*	*0*	*0*	14.2	0	0	0	0
	2	52	4.35	12.2	0	0	0	0	*12.2*	*0*	*0*	*0*	*0*	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	6.51	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*	14.1	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	4984	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} x 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 x 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} x 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: $Y = D + D^2 + S + A + YR + A.YR$, 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).

	Year				
	1984	1988	1989	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 1 eggs.

	Standard area							
Survey year	#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 $\log_n$ 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 (x 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 ln gutted weight for sole from 1Vb west and V11d over the period 1988-1991.

	INTERCEPT		SLOPE	
	IVb	VIId	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	df	MS	F	Pr>F
ln 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 fec=a(ar,yr) + b(yr)ln gwt
- RSS due to model of ln fec=a(ar,yr) + b(ar+yr)ln(ln gwt)
Year SS derived from: RSS due to model of ln fec=a(ar,yr)+b(ar)ln gwt
-RSS due to model of ln fec=a(ar,yr)=b(ar+yr)ln gwt
where ln fec =ln fecundity, ln gwt =ln gutted weight, ar=area,yr=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 (east)	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

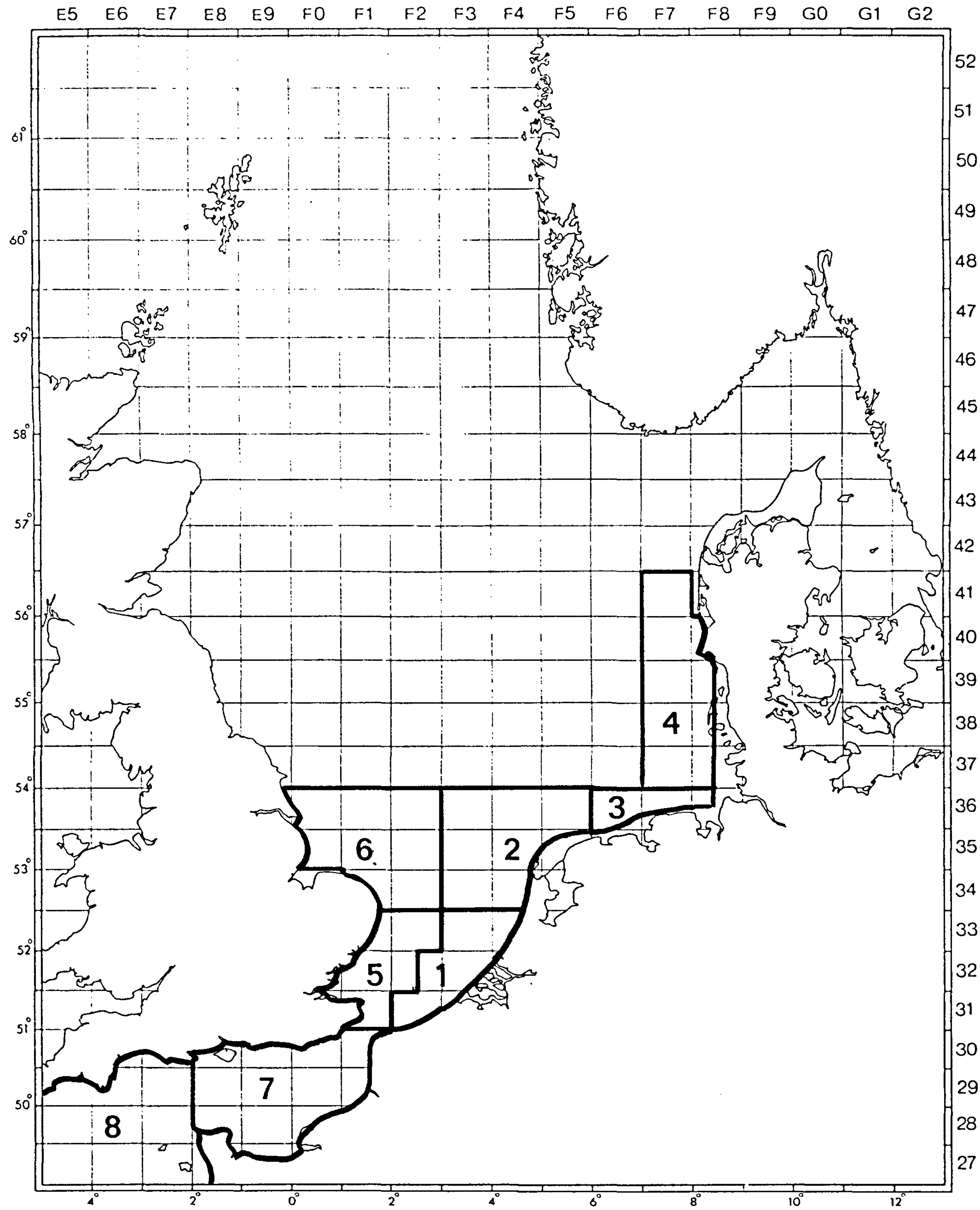
Table 5.1.3. Estimate of female spawning stock biomass for VIId sole in 1991.

Age	Stock numbers 1-1-1991 (thousands)	Z-q1	Stock numbers 1-4-1991 (thousands)	Sex-ratio	Maturity	Weight Q2 (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
Total							3093

Table 5.1.4. 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 (kg)	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



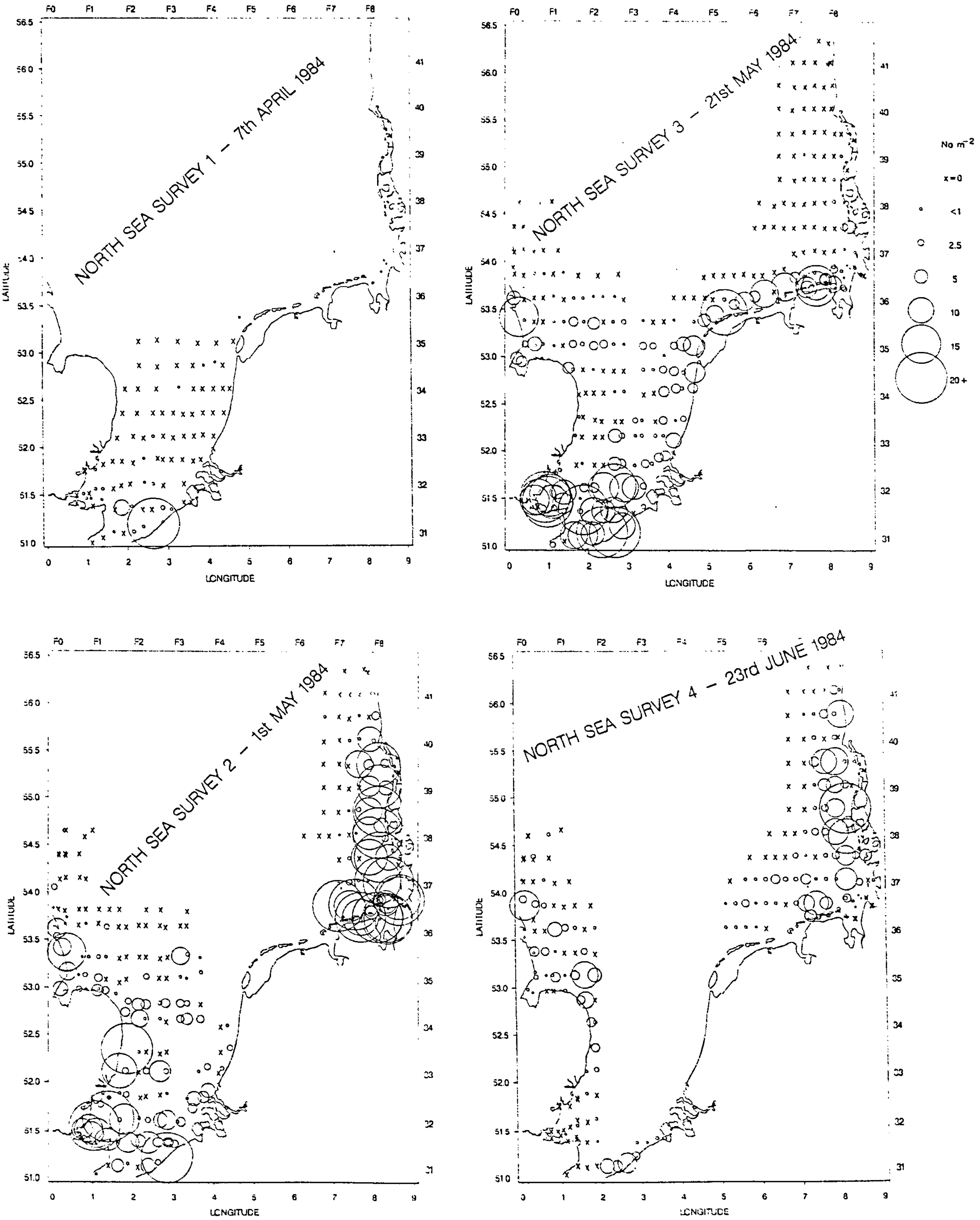
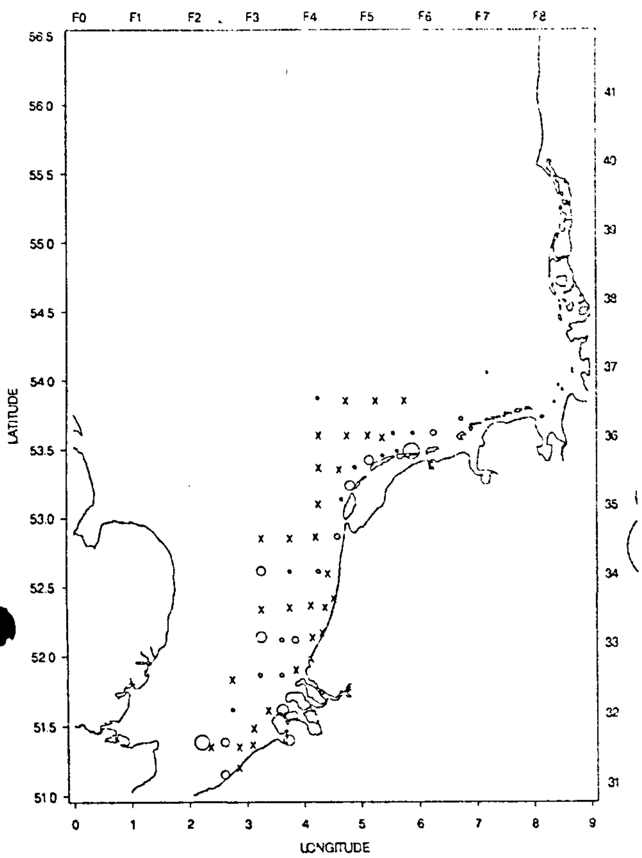
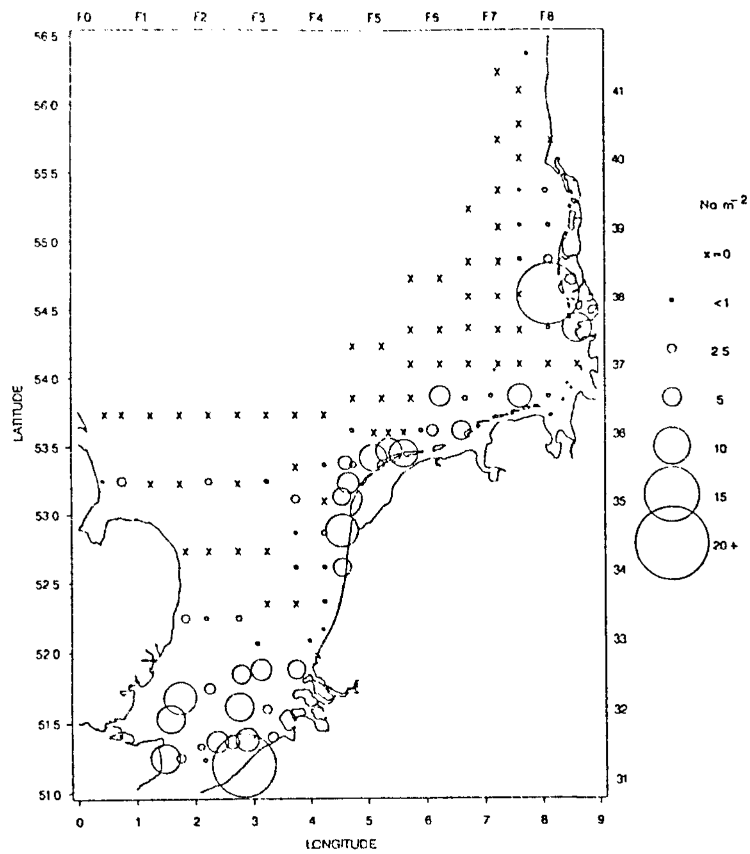


Figure 3.2.1. Distribution of stage 1 eggs of North Sea Sole in 1984

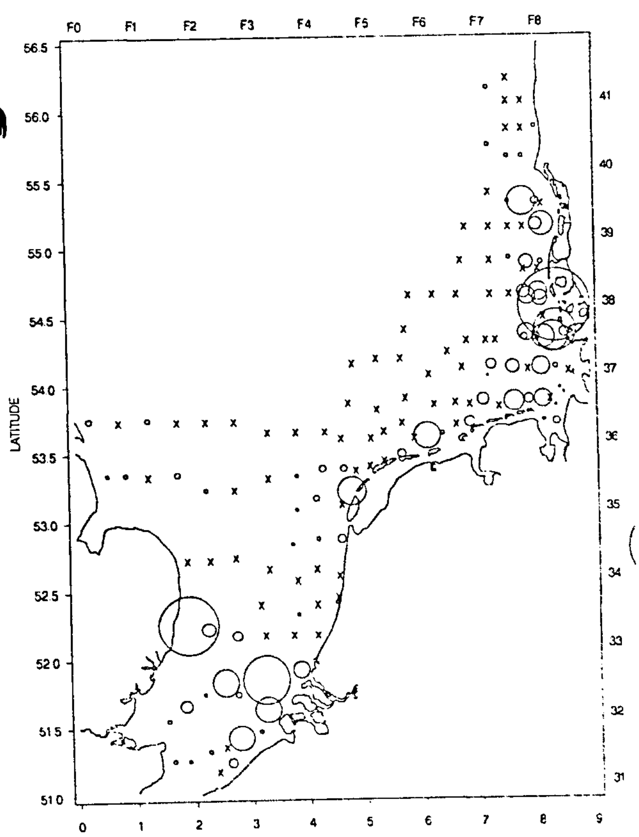
NORTH SEA SURVEY 1 – 8th APRIL 1988



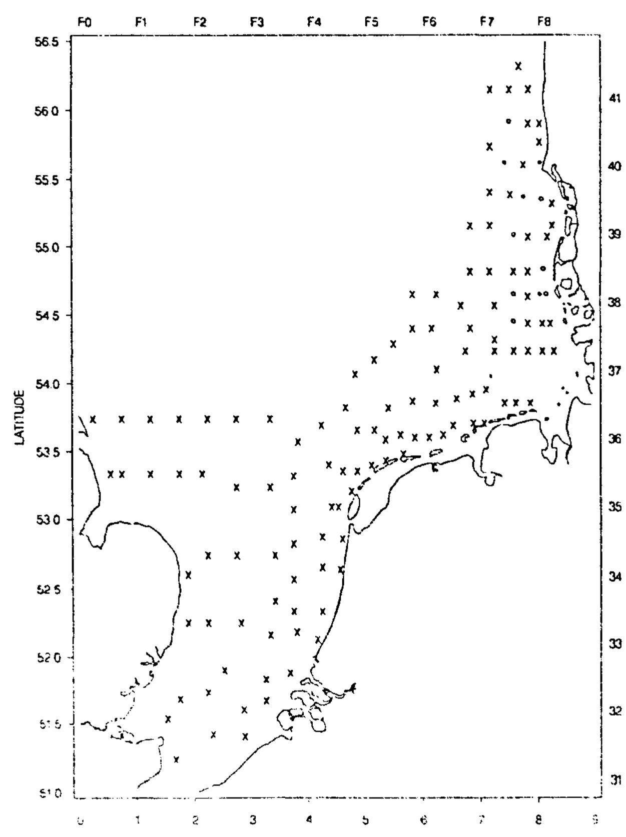
NORTH SEA SURVEY 2 – 30th APRIL 1988



NORTH SEA SURVEY 3 – 24th MAY 1988



NORTH SEA SURVEY 4 – 24th JUNE 1988



NORTH SEA SURVEY 5 – 23rd JULY 1938

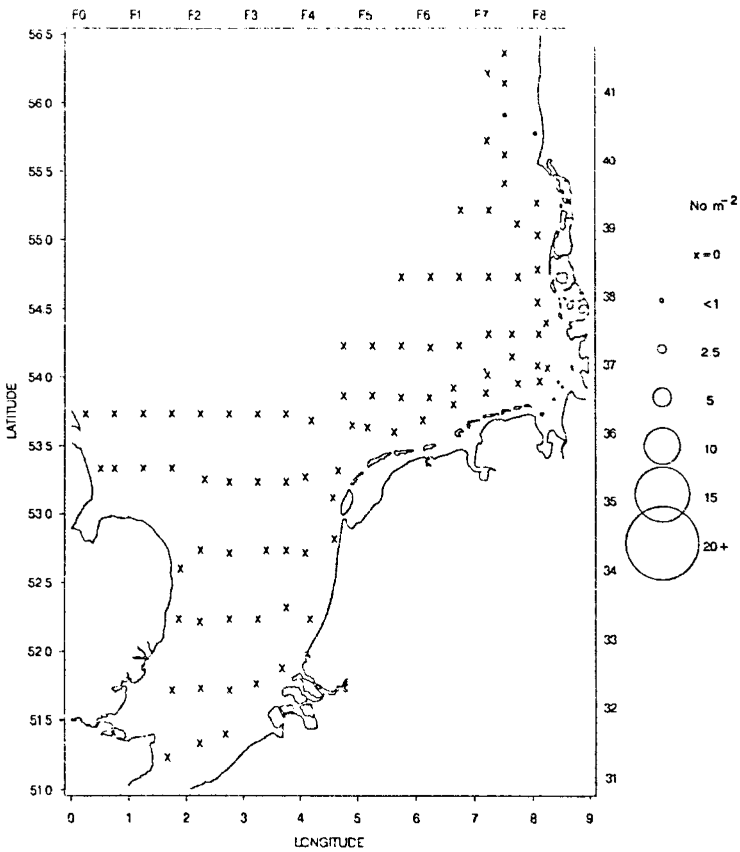
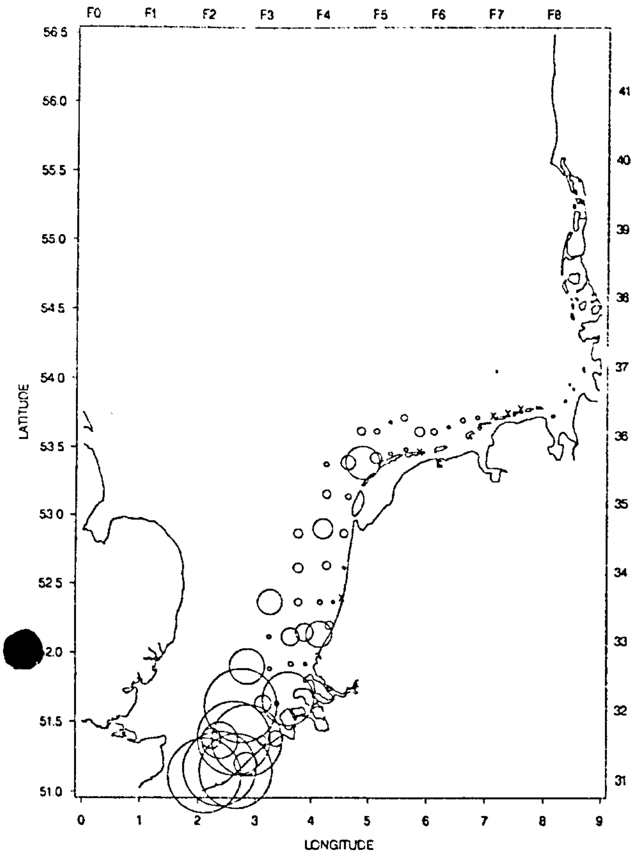
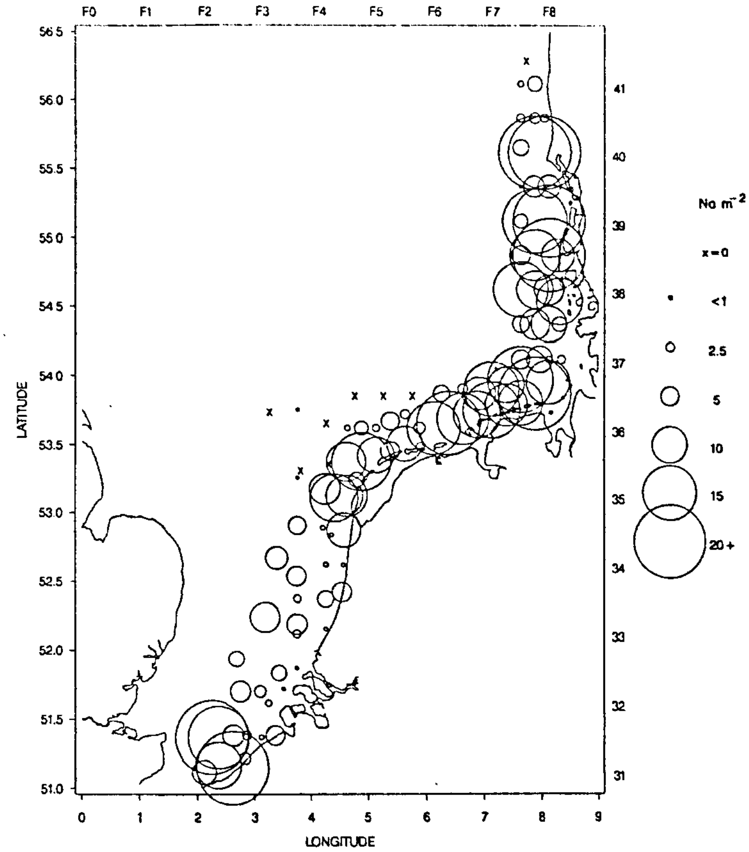


Figure 3.2.2. Distribution of stage 1 eggs of North Sea sole in 1988.

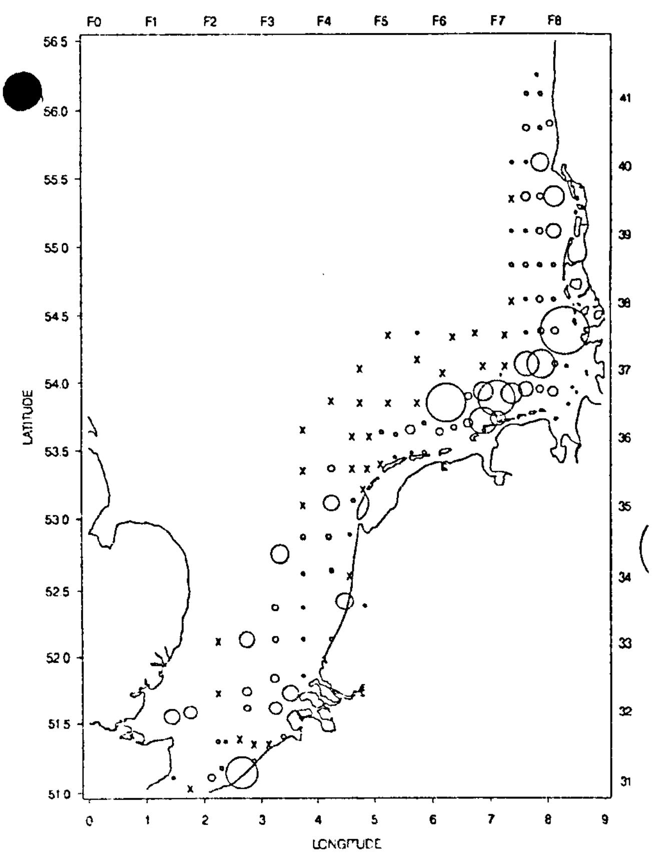
NORTH SEA SURVEY 1 – 14th APRIL 1989



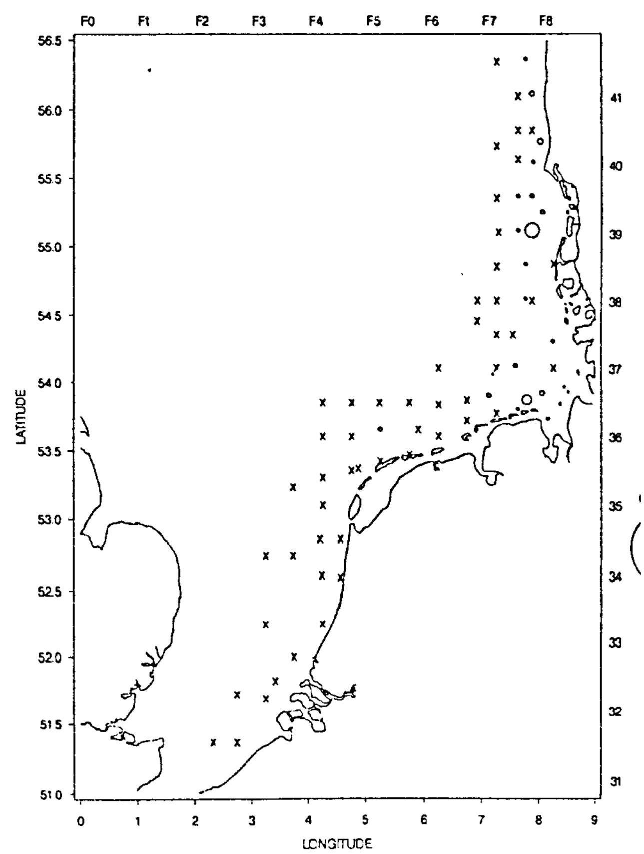
NORTH SEA SURVEY 2 – 28th MARCH 1989



NORTH SEA SURVEY 3 – 29th MAY 1989



NORTH SEA SURVEY 4 – 23rd JUNE 1989



NORTH SEA SURVEY 5 – 13th JULY 1989

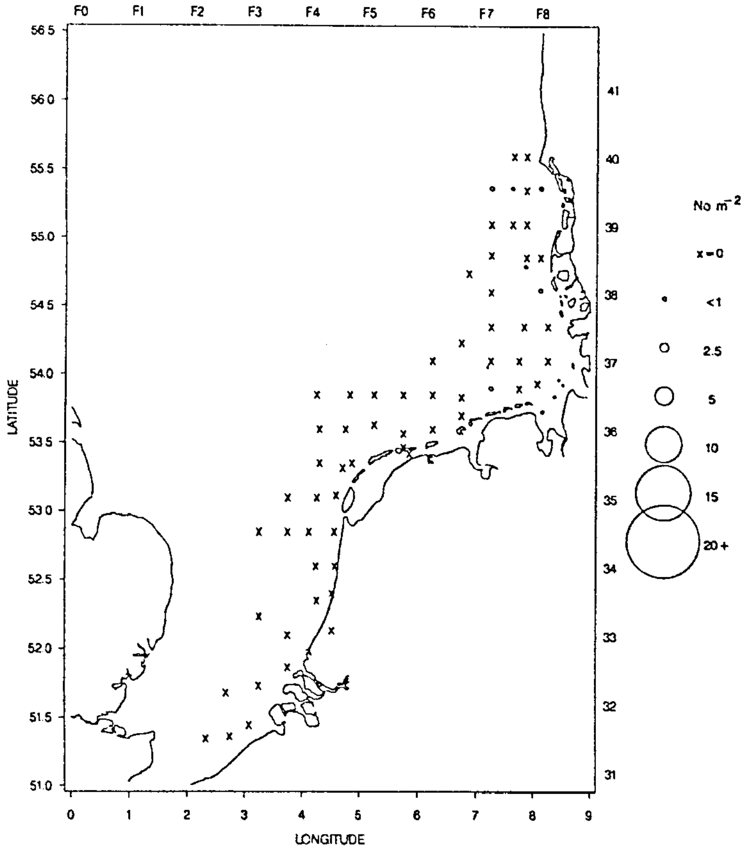
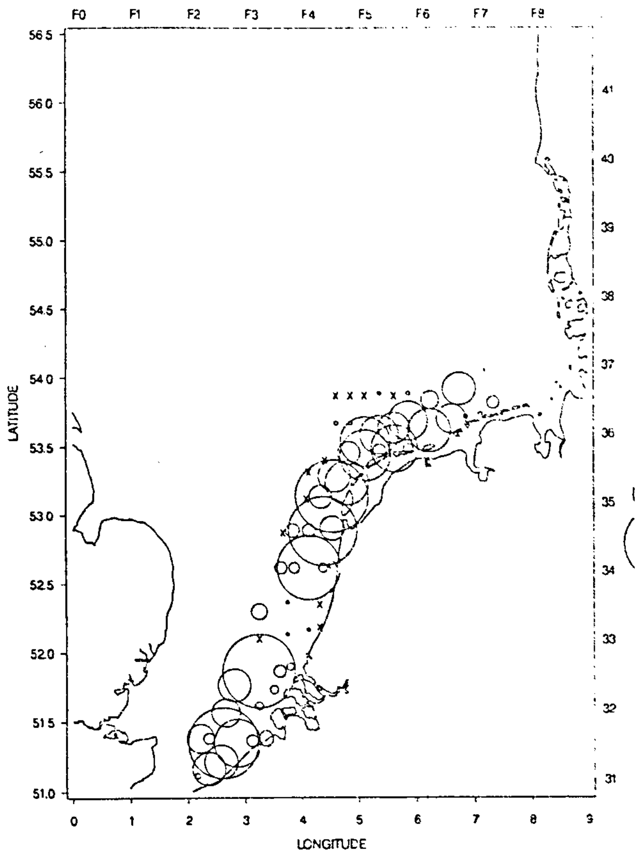
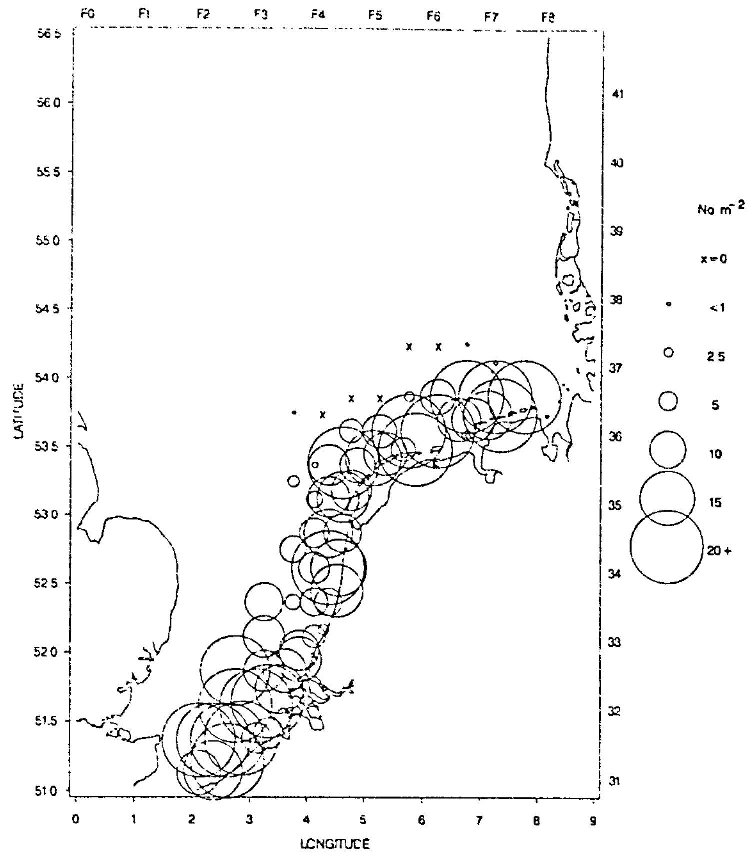


Figure 3.2.3. Distribution of stage 1 eggs of North Sea sole in 1989.

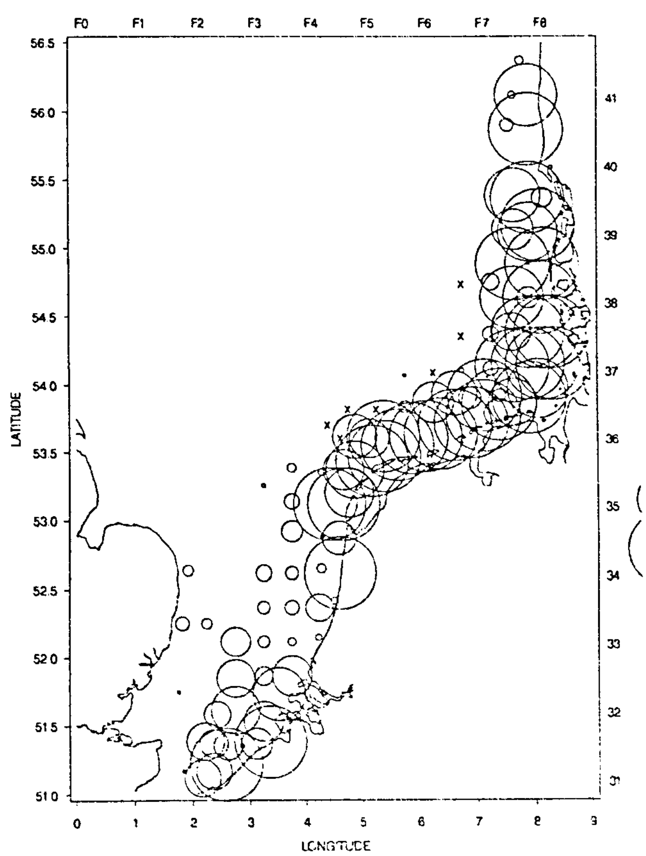
NORTH SEA SURVEY 1 – 13th MARCH 1990



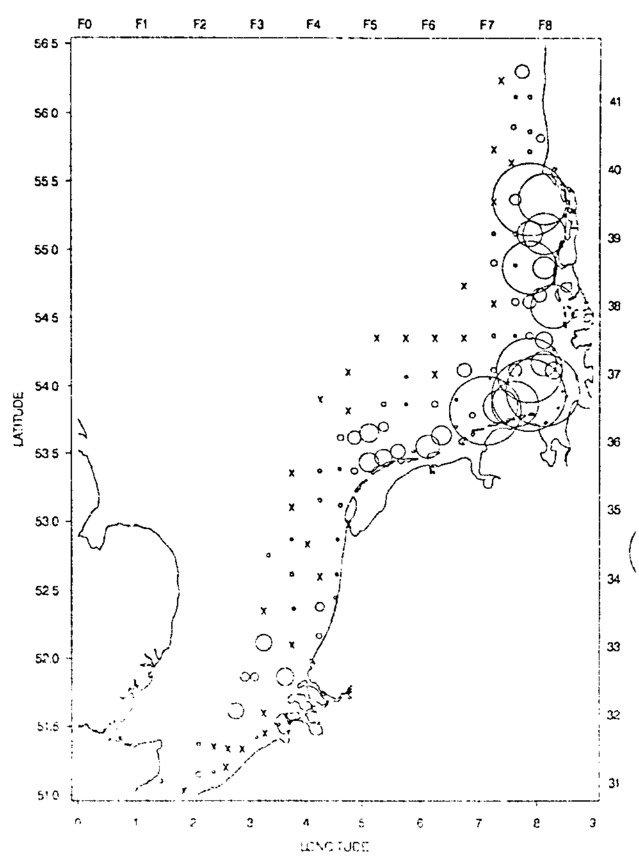
NORTH SEA SURVEY 2 – 28th MARCH 1990



NORTH SEA SURVEY 3 – 28th APRIL 1990



NORTH SEA SURVEY 4 – 28th MAY 1990



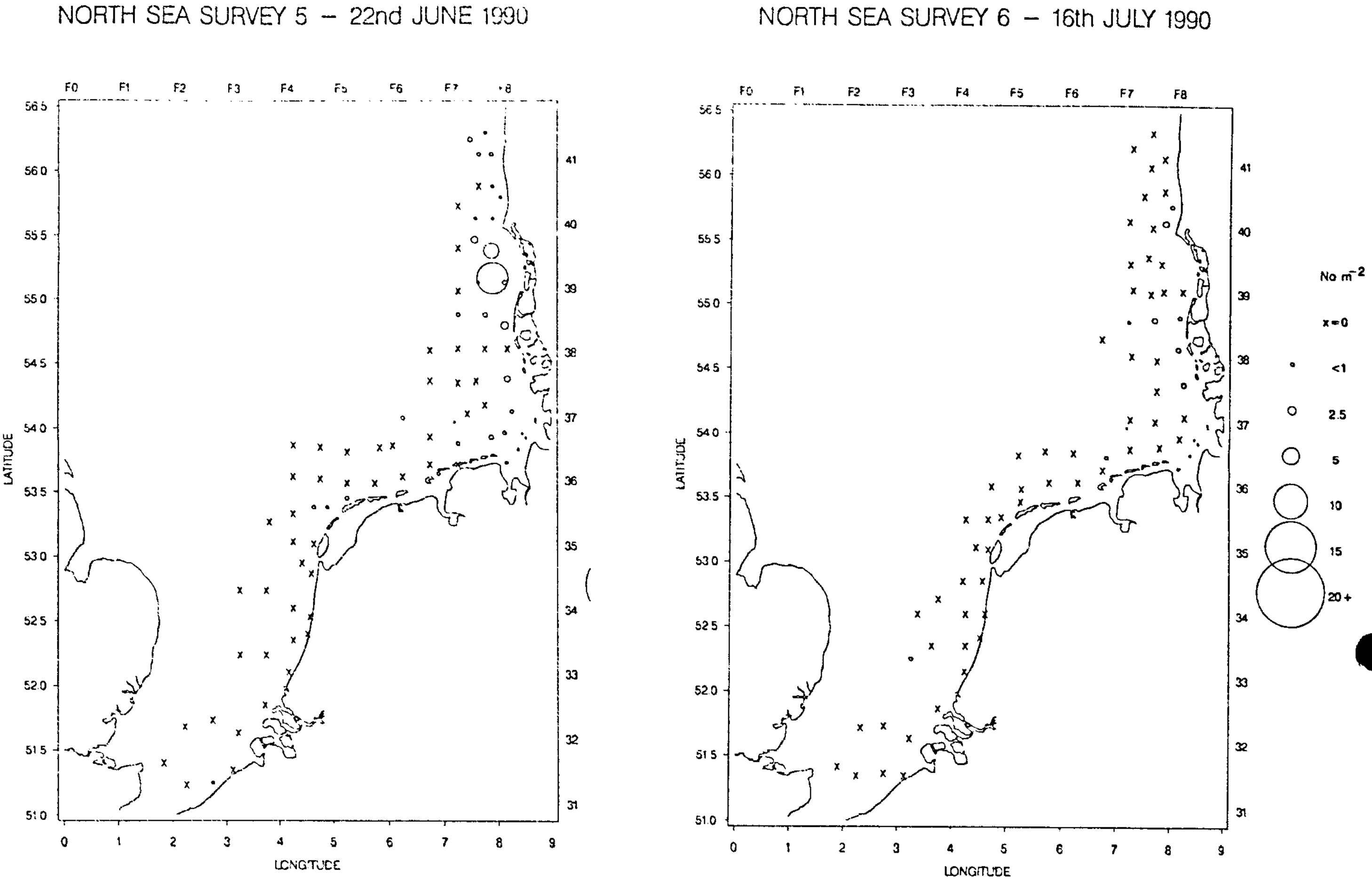
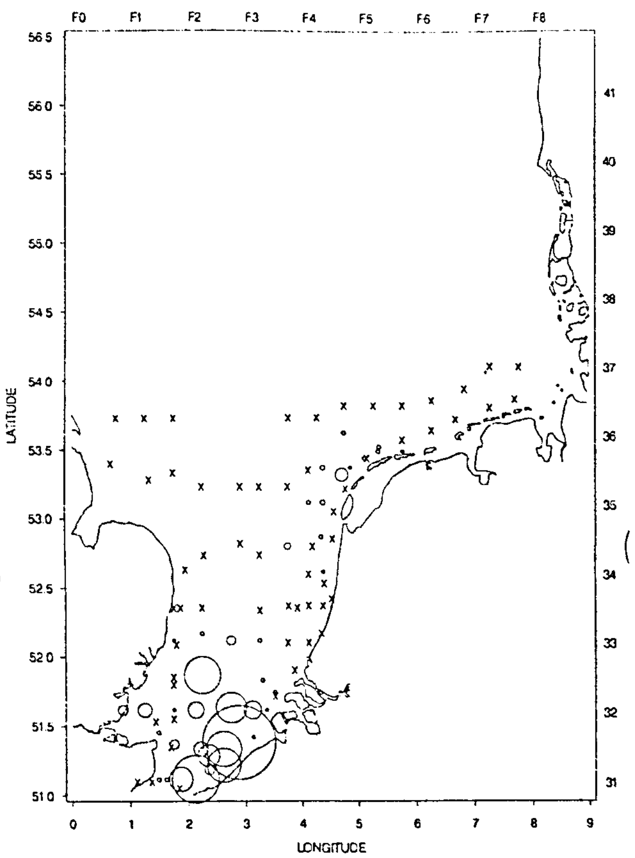
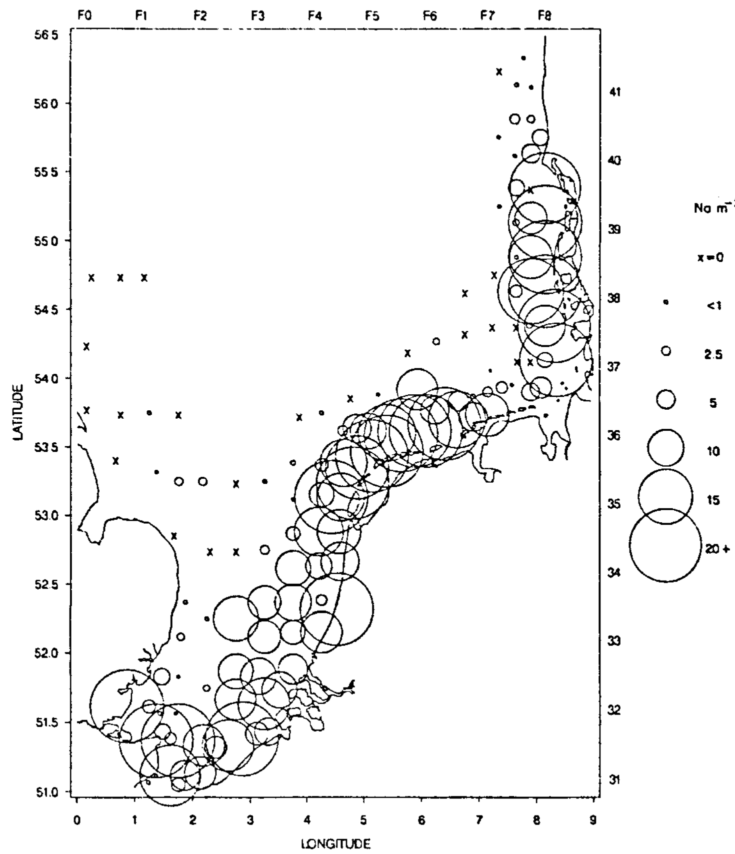


Figure 3.2.4. Distribution of stage 1 eggs of North Sea sole in 1990.

NORTH SEA SURVEY 2 – 20th MARCH 1991



NORTH SEA SURVEY 3 – 20th APRIL 1991



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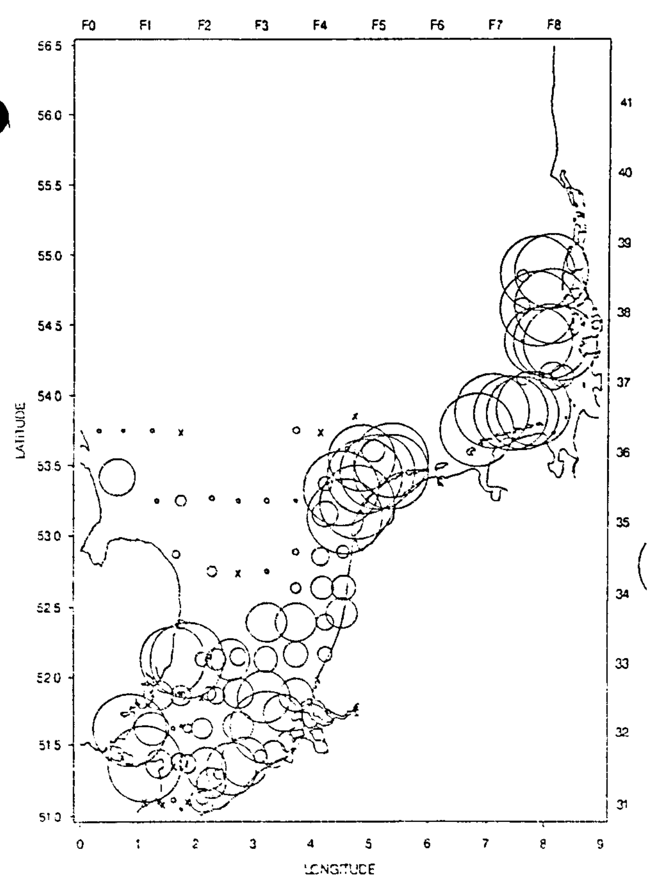
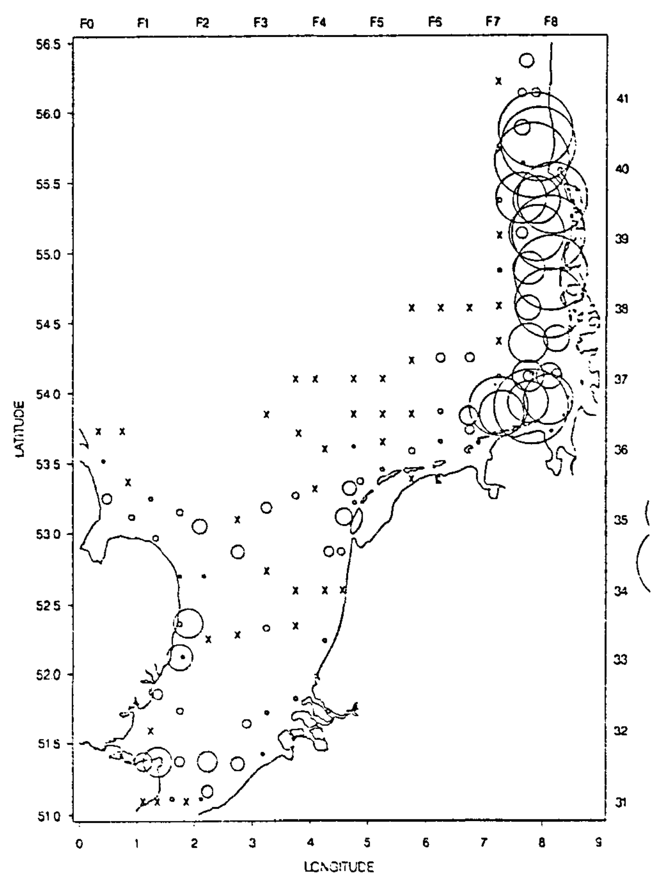


NORTH SEA SURVEY 5 – 12th JUNE 1991



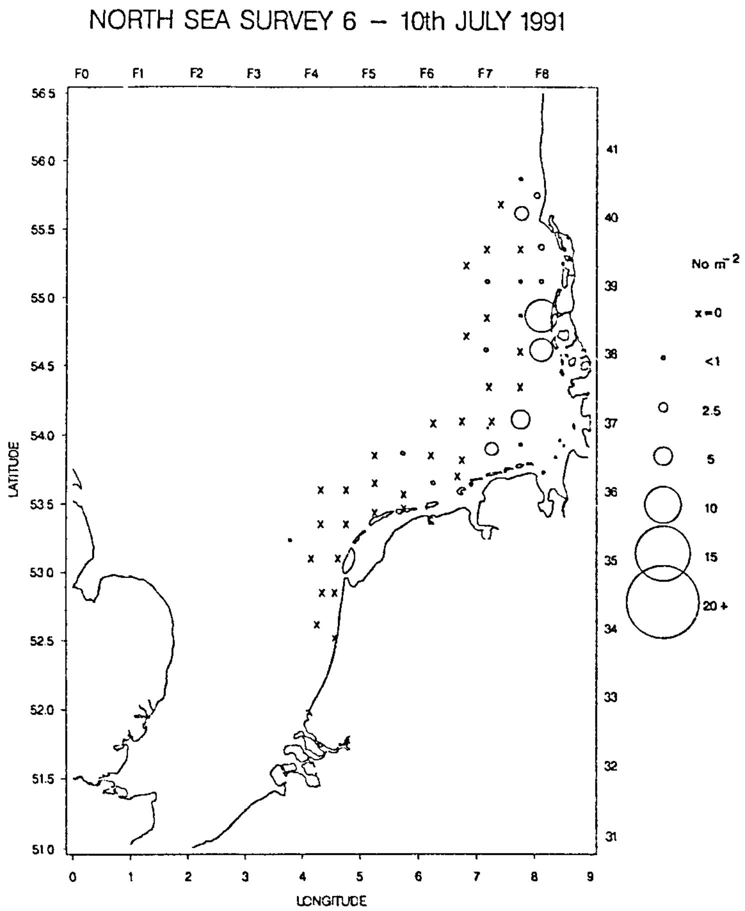
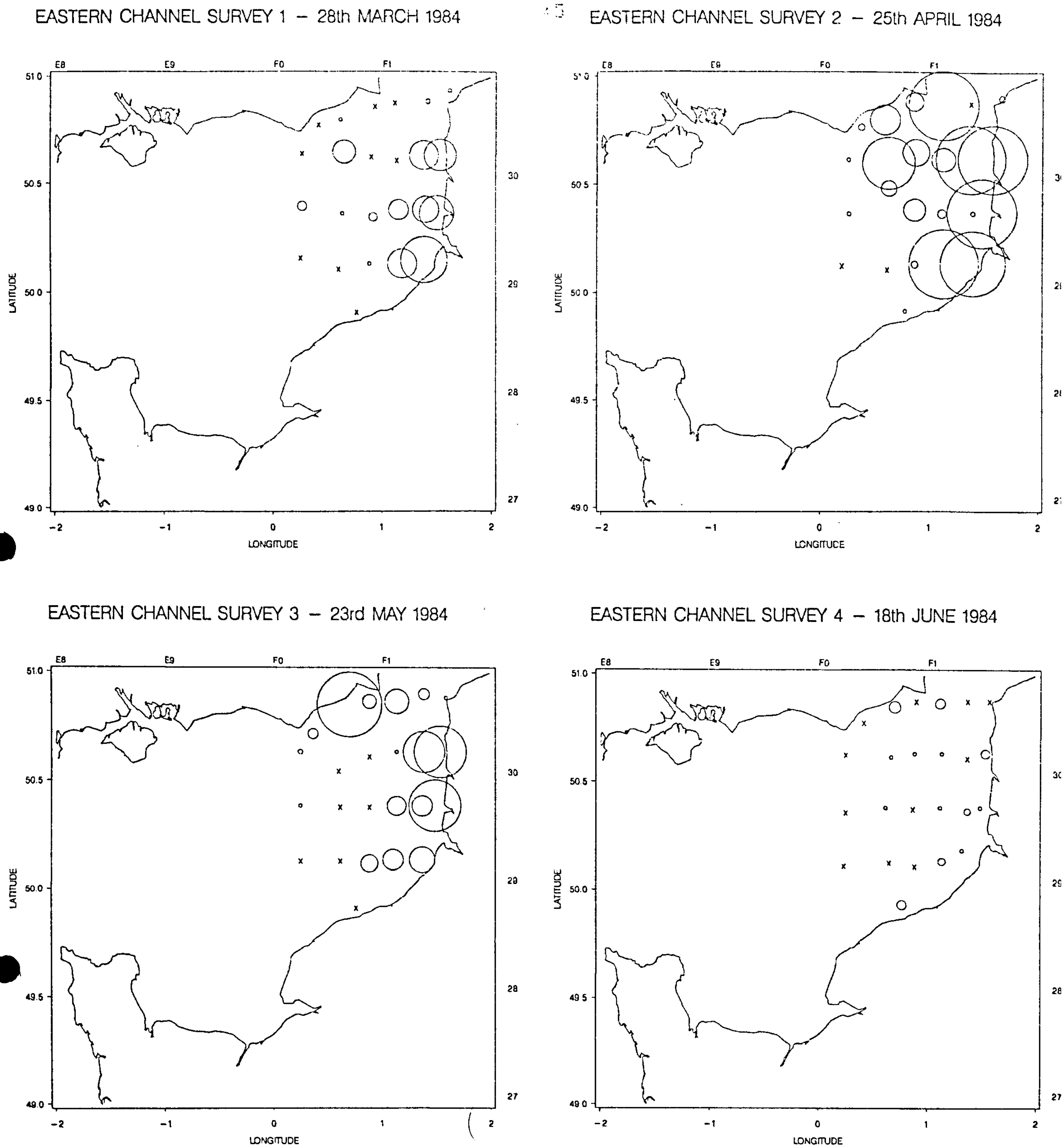


Figure 3.2.5. Distribution of stage 1 eggs of North Sea sole in 1991.



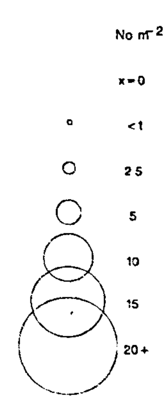
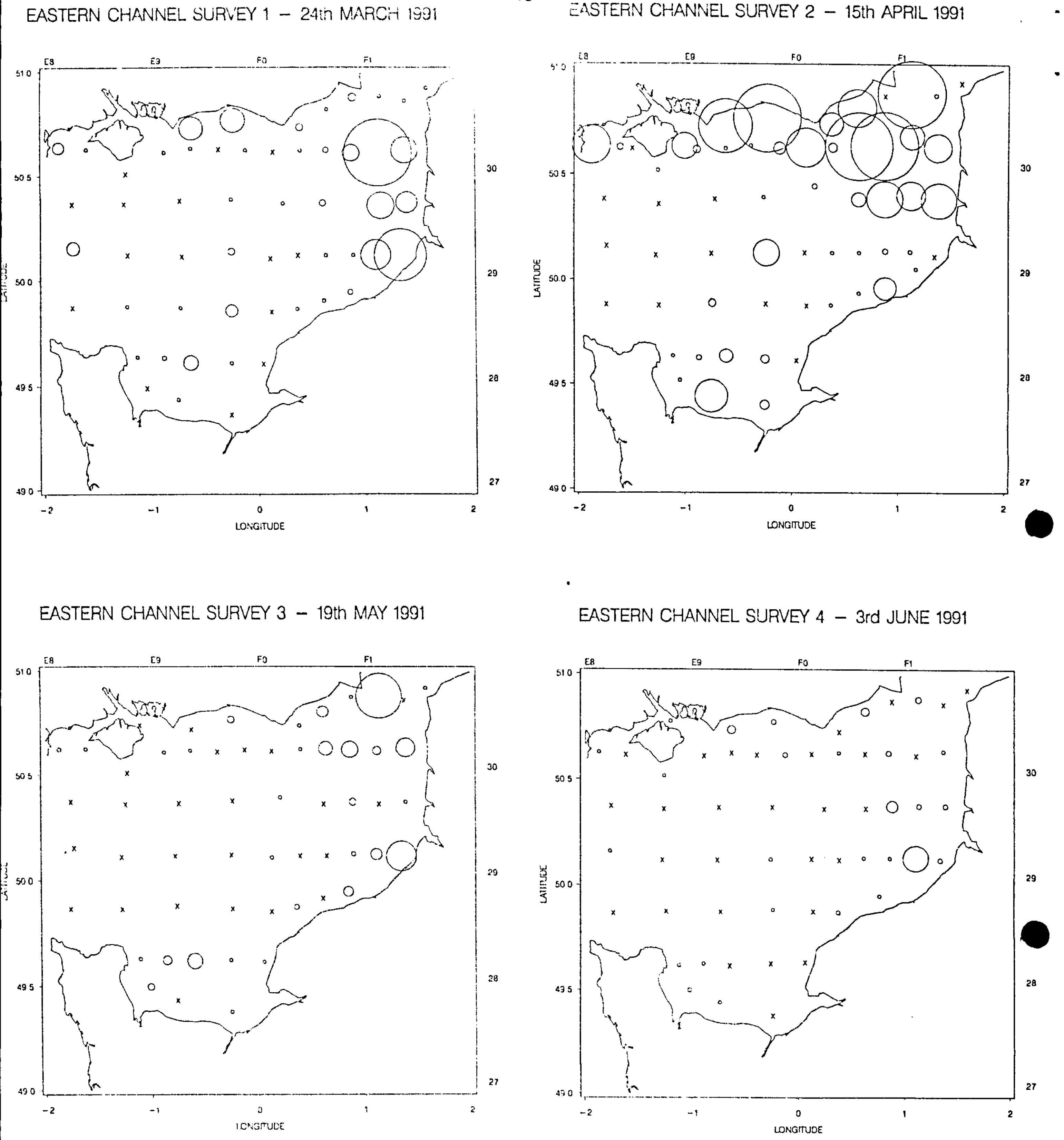


Figure 3.2.6. Distribution of stage 1 eggs of sole in the eastern English Channel (VIId) in 1984.



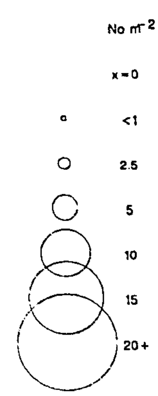
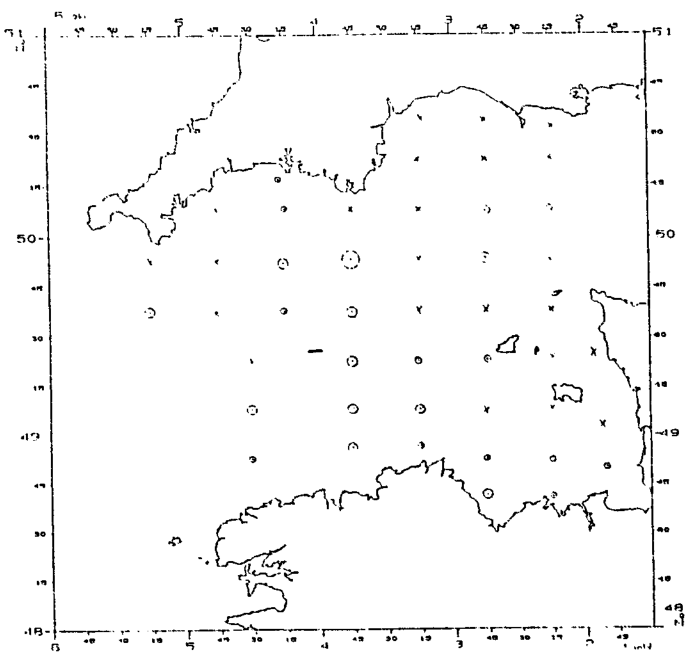


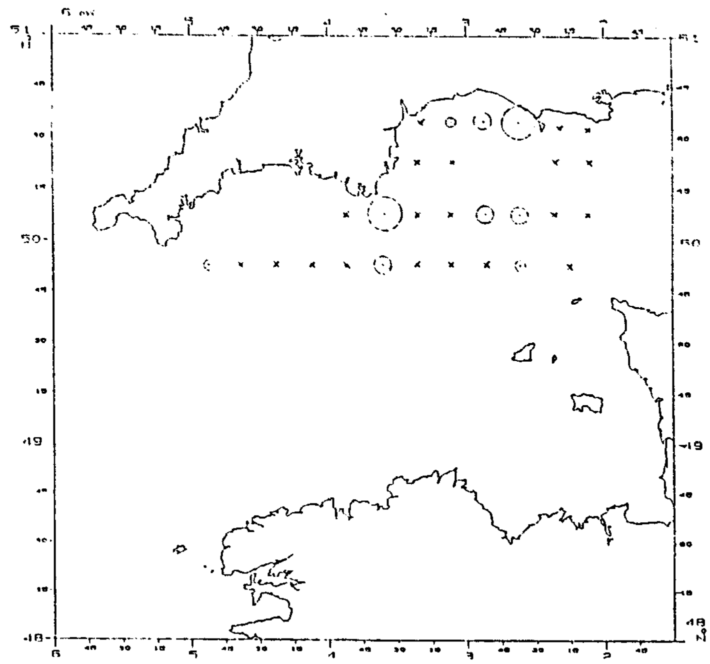
Figure 3.2.7. Distribution of stage 1 eggs of sole in the eastern English Channel (VIId) in 1991.

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

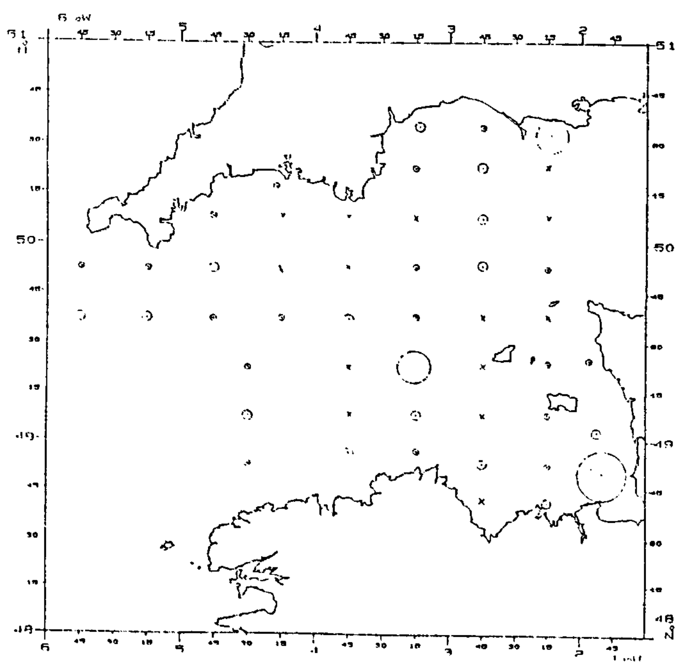
WESTERN CHANNEL SURVEY 1 - 1st MARCH 1991



WESTERN CHANNEL SURVEY 2 - 20th MARCH 1991



WESTERN CHANNEL SURVEY 3 - 21ST APRIL 1991



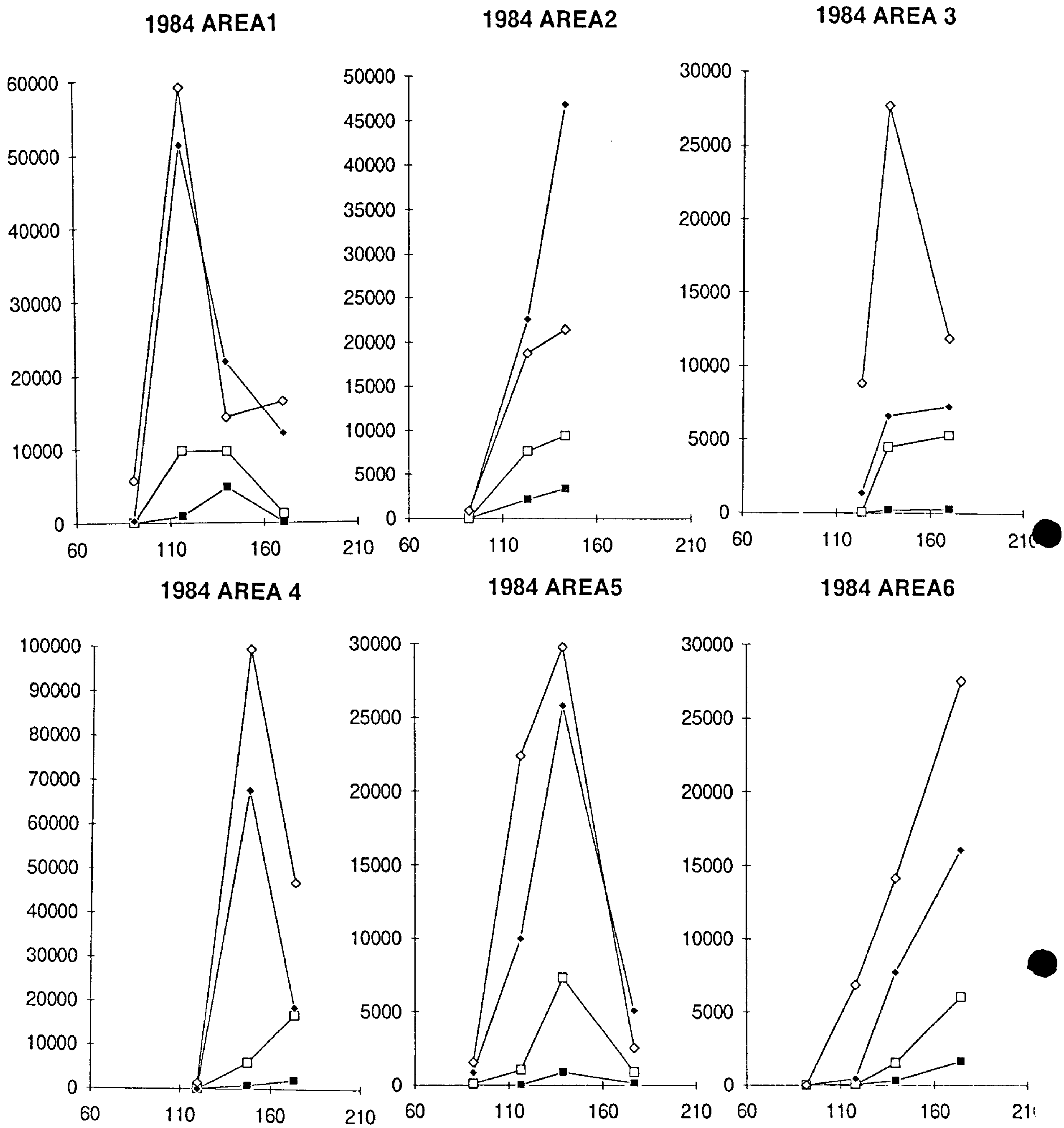


Figure 3.4.1. Production curve (N.day-1) of sole eggs in 1984 in the standard areas #1 - #6 of the North Sea

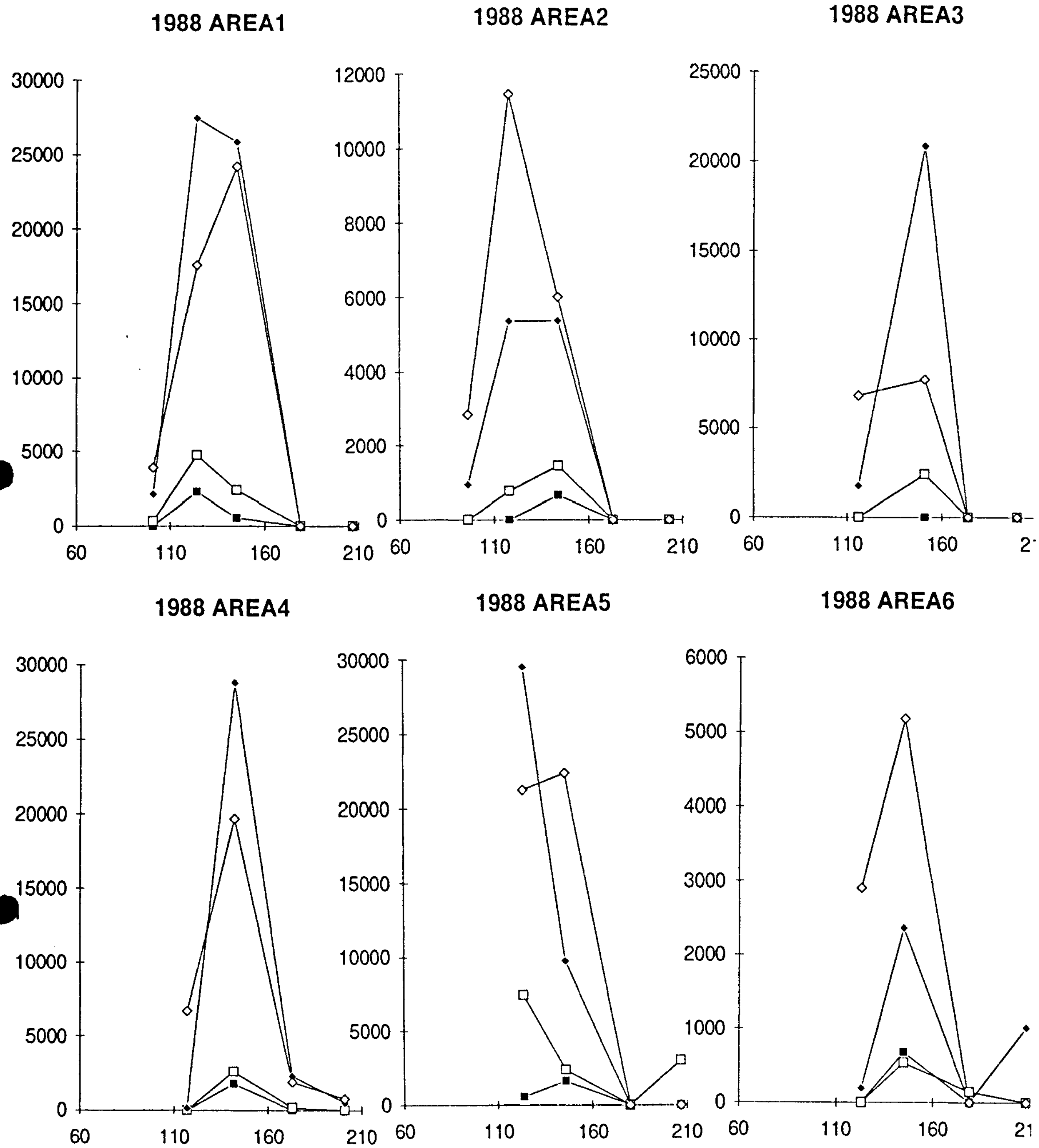


Figure 3.4.2. Production curve (N.day-1) of sole eggs in 1988 in the standard areas #1 - #6 of the North Sea

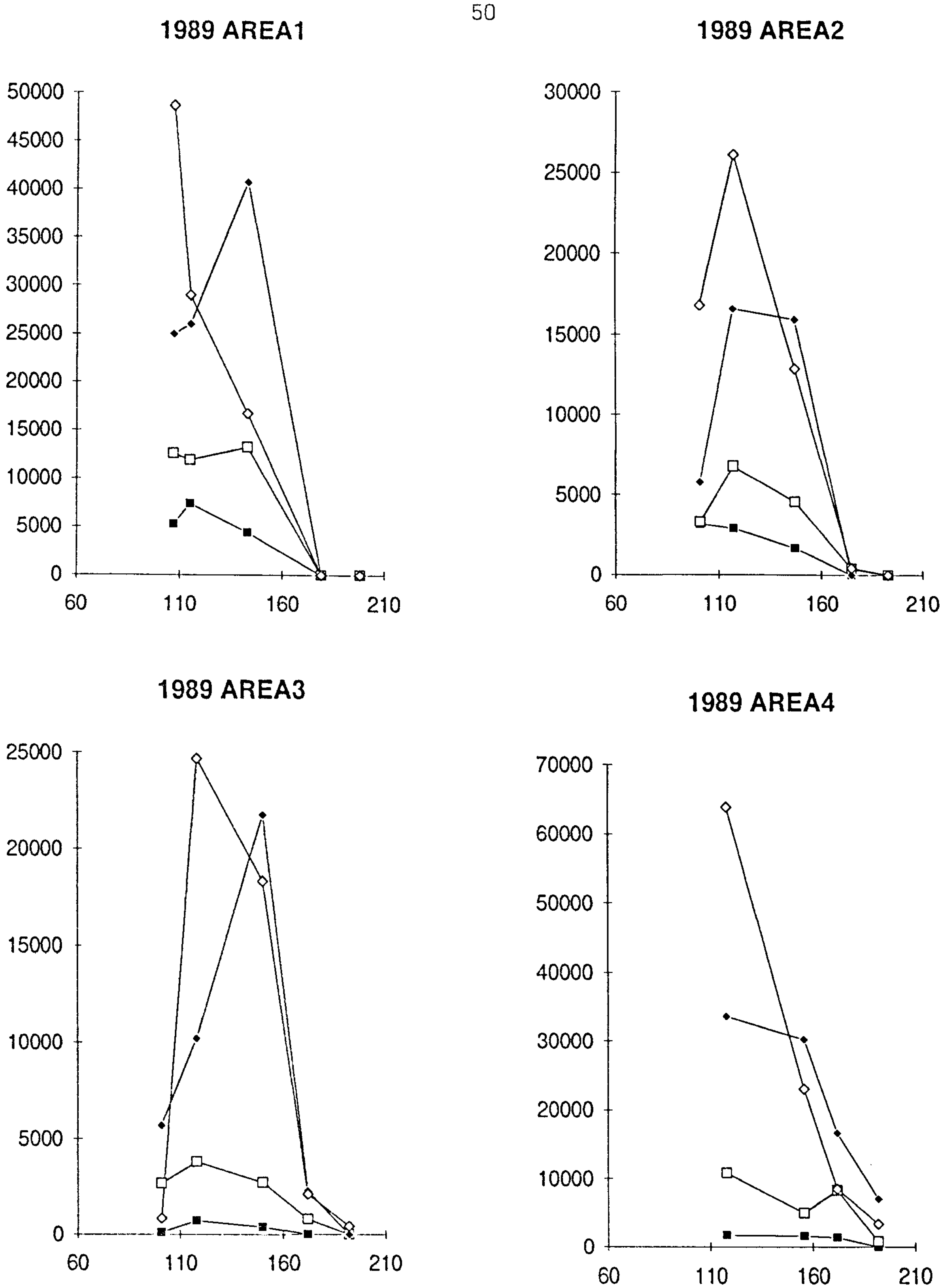


Figure 3.4.J . Production curve (N.day-1) of sole eggs in 1989 in the standard areas #1 - #4 of the North Sea

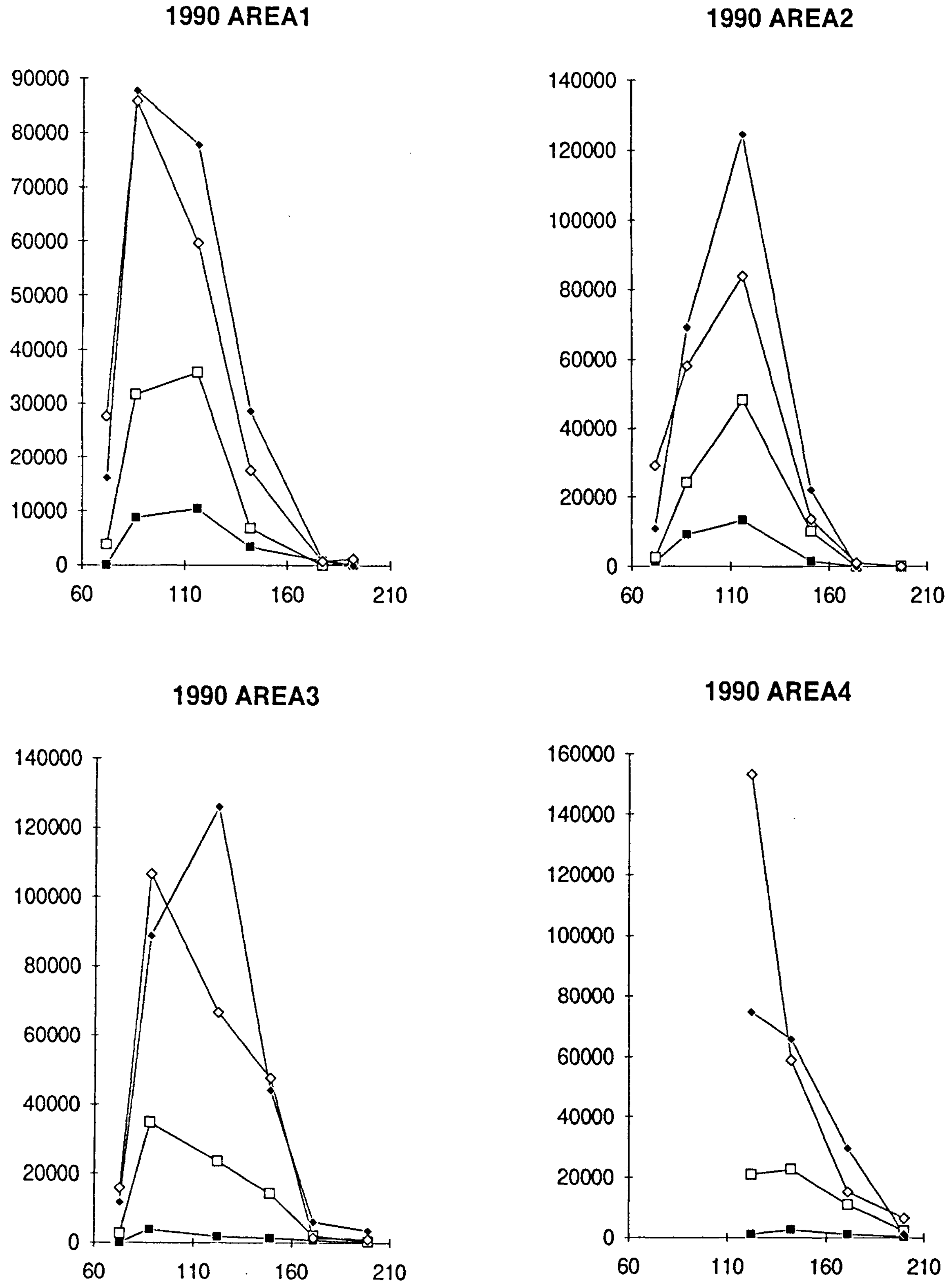


Figure 3.4.4. Production curve (N.day-1) of sole eggs in 1990 in the standard areas #1 - #6 of the North Sea

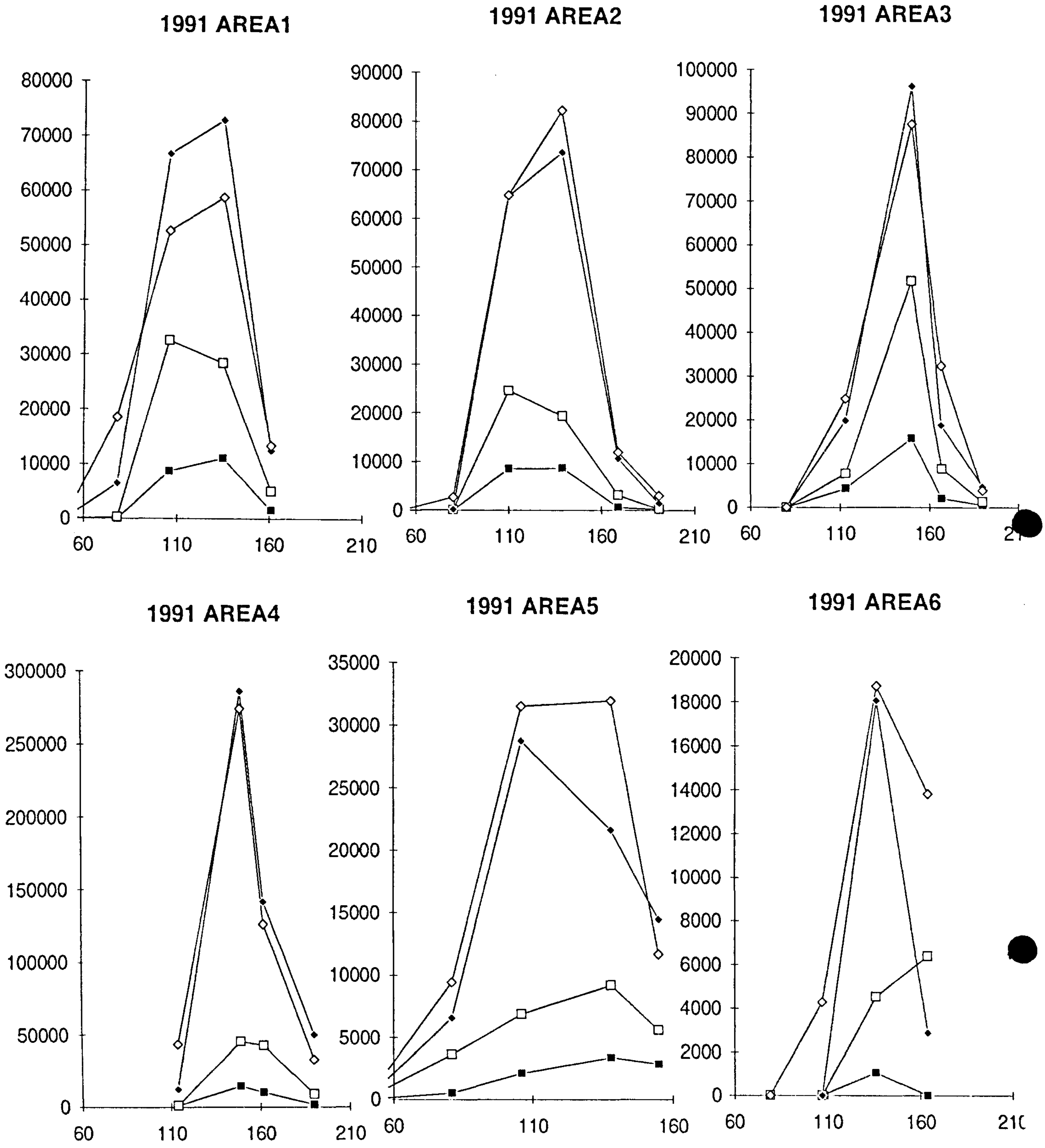
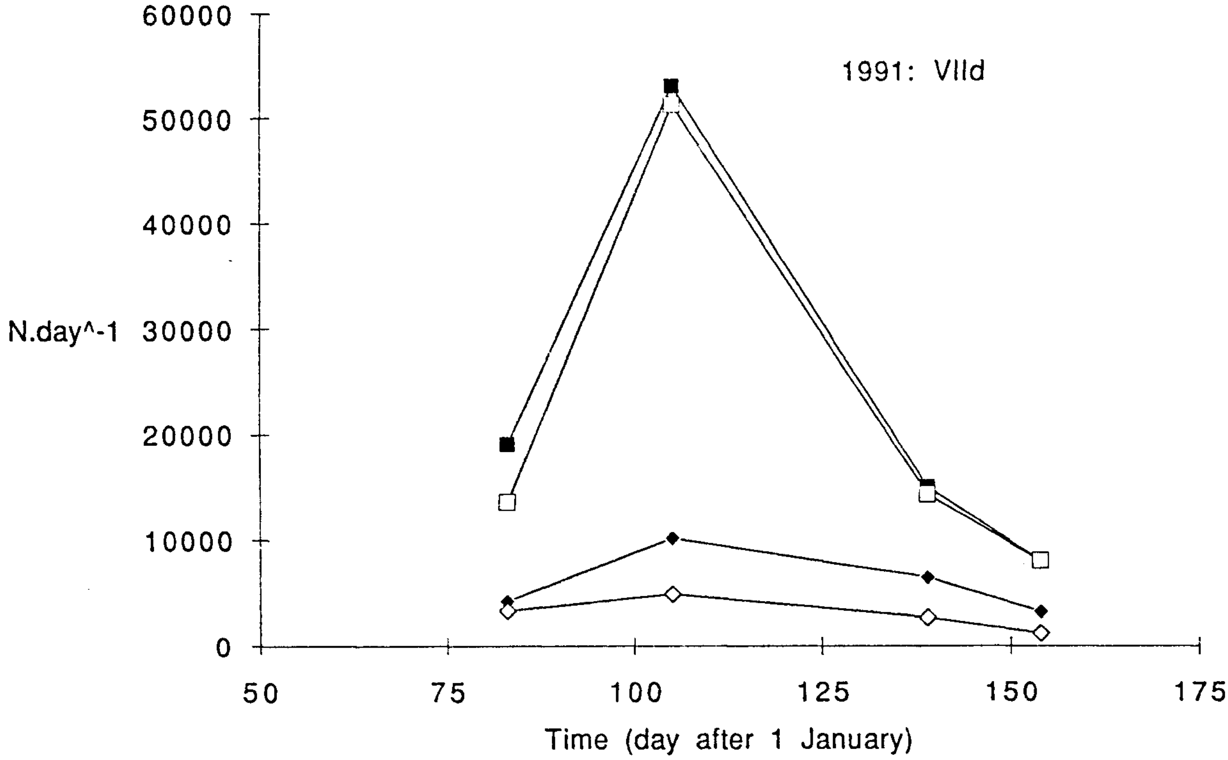


Figure 3.4.5. Production curve (N.day-1) of sole eggs in 1991 in the standard areas #1 - #6 of the North Sea



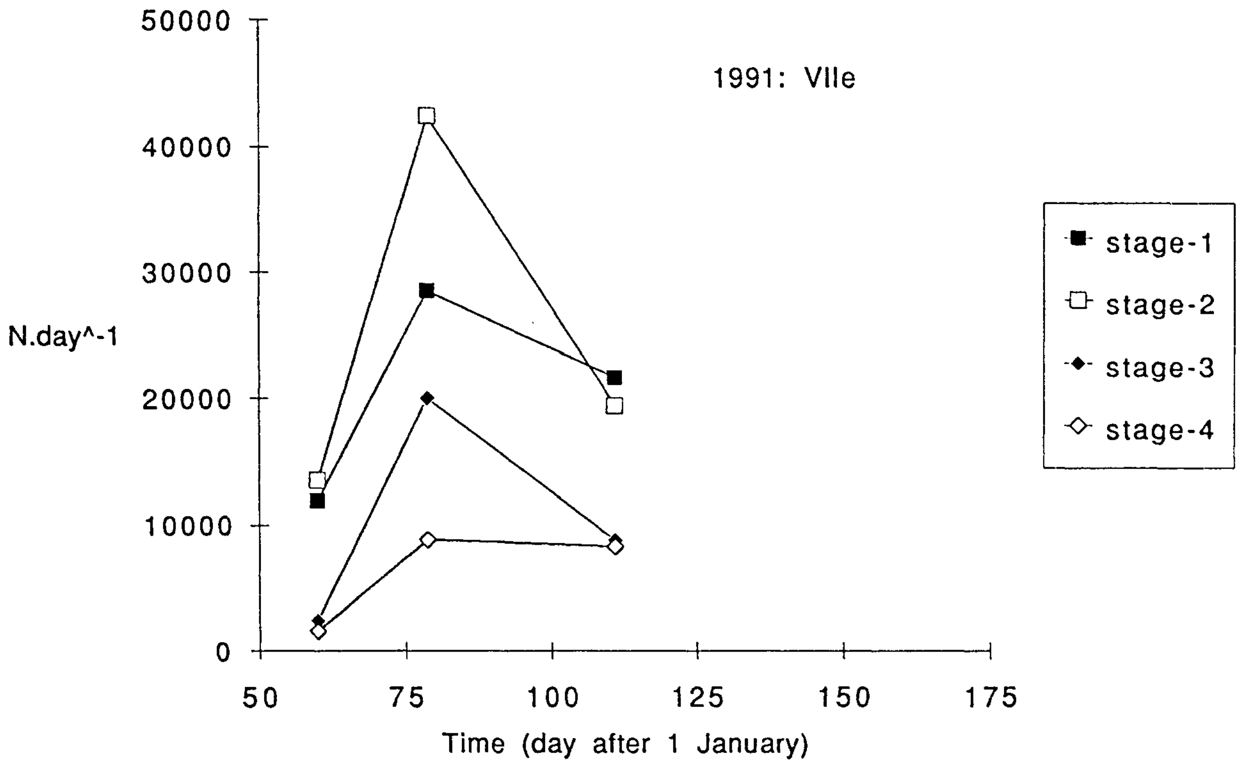


Figure 3.4.6. Production curve (N.day-1) of sole eggs in 1991 in the eastern English Channel (#7) and western English Channel (#8)

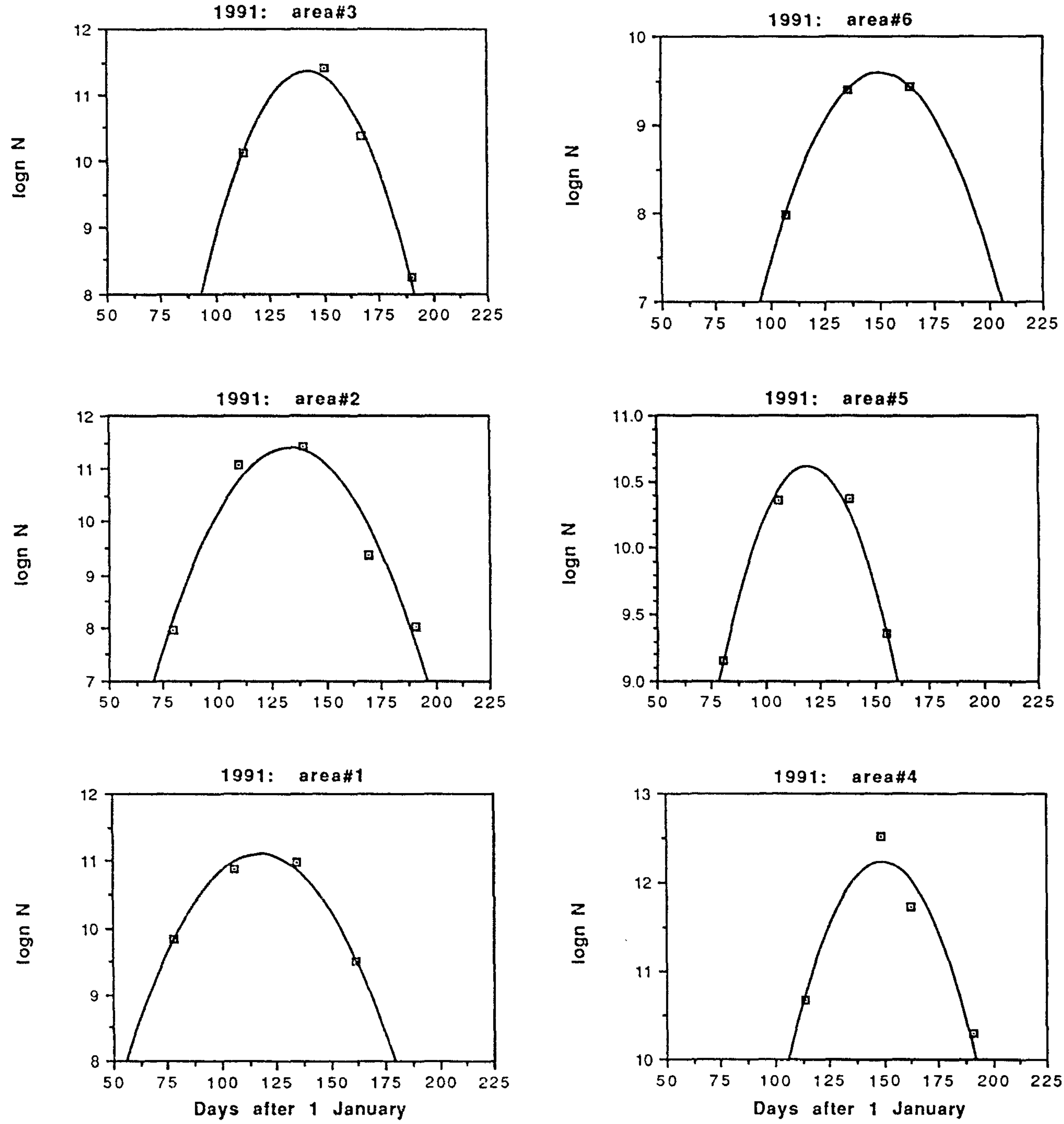


Figure 3.4.7. Parabolic regressions through the logn daily egg production of stage 1 against time (days after 1 January) in the standard areas (#1 - #6) in the North Sea in 1991.

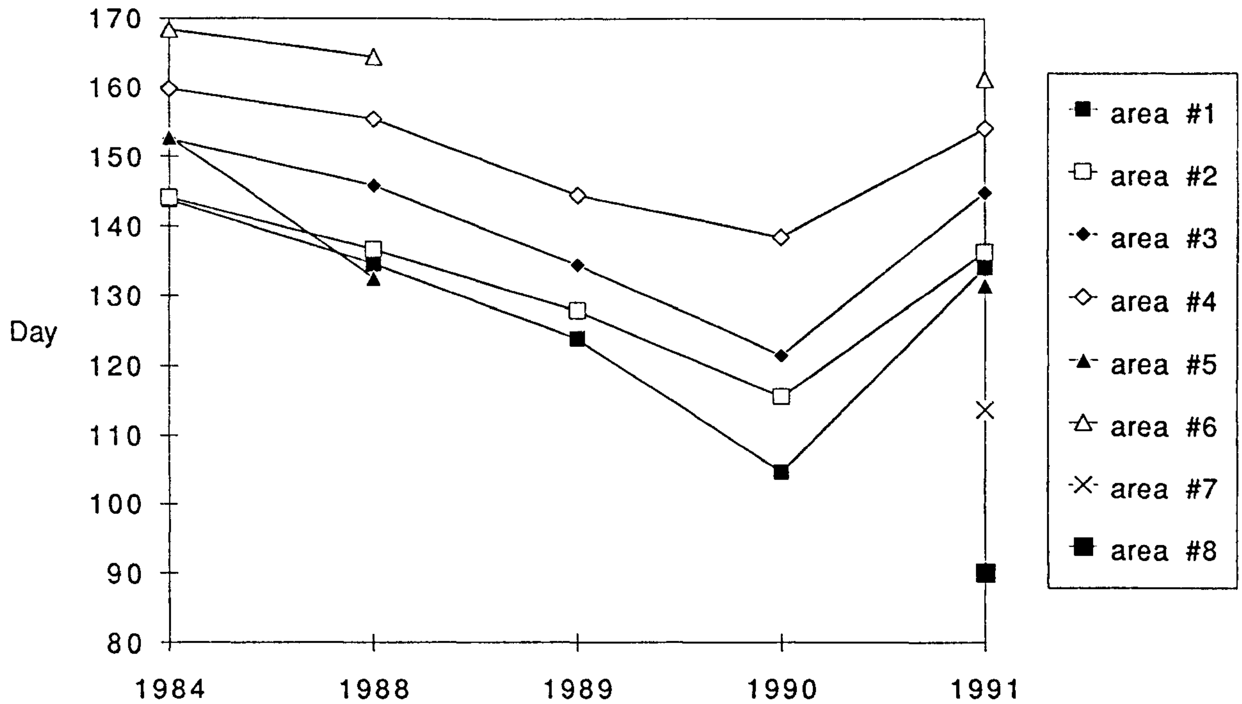


Figure 3.4.8. Annual and geographical differences in the time of peak spawning (day after 1 January)

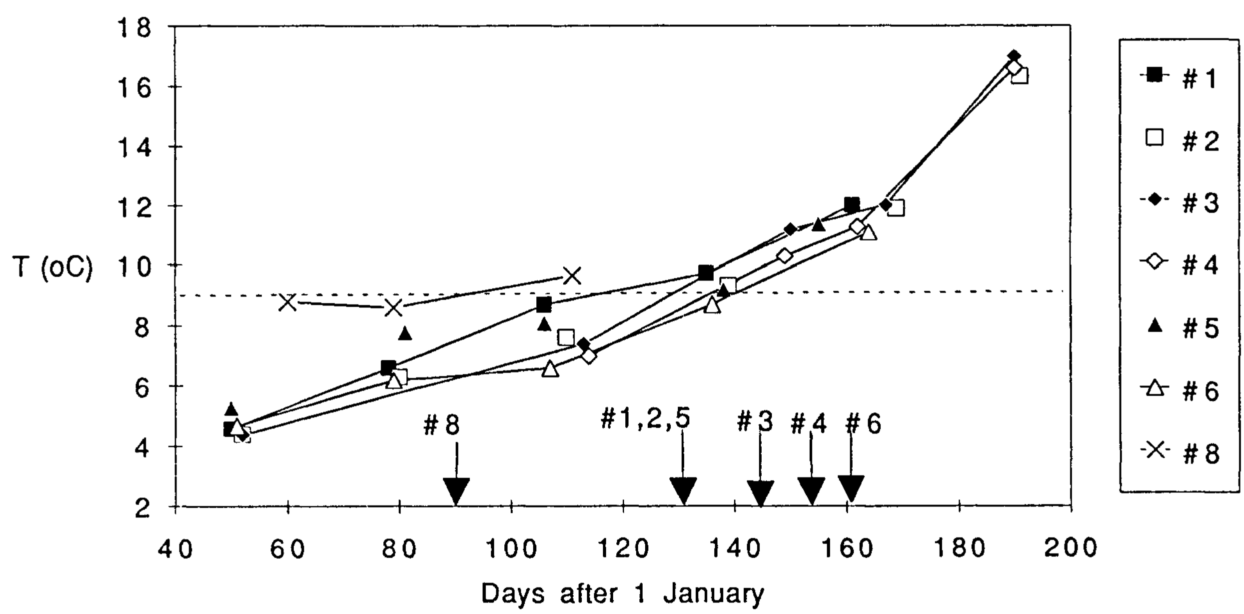


Figure 3.4.9. Spring increase in water temperature and the timing of the peak of spawning in 1991 in the North Sea (areas #1 - #6) and western English Channel (VIIe).

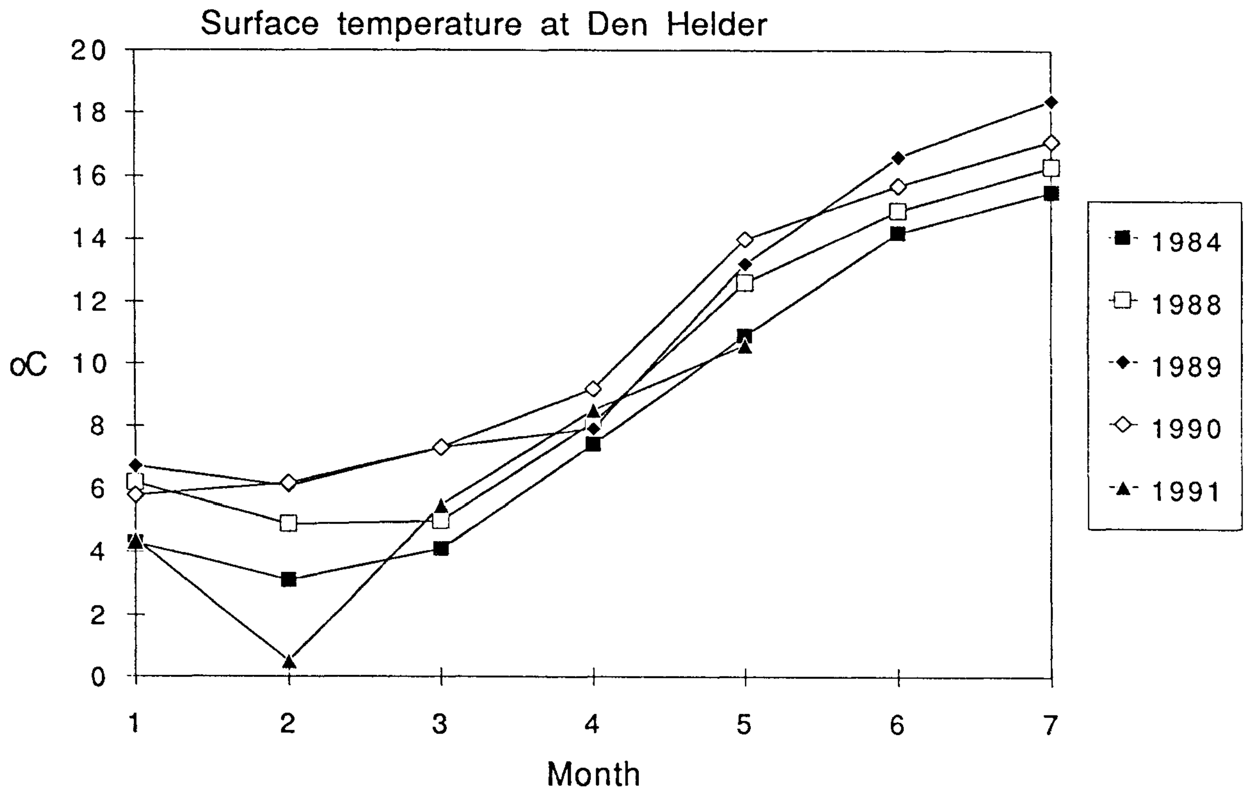


Figure 3.4.10 Differences in the increase in sea temperature illustrated by the average monthly temperature at a station in the entrance of the western Wadden Sea (den Helder)

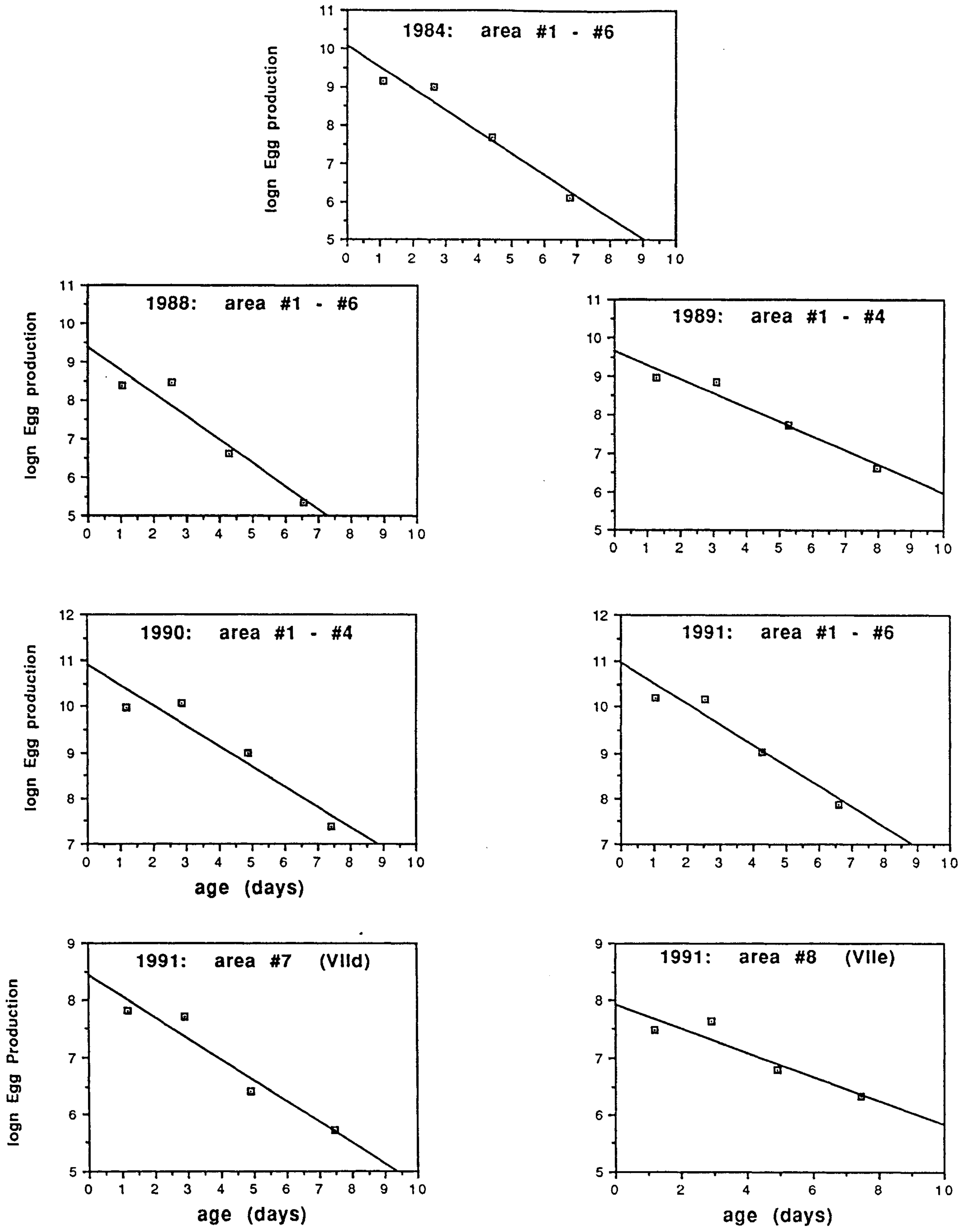


Figure 3.5.1. Plots of the $\log_n$ Egg production against mean age of stage 1, 2, 3 and 4 eggs for different years in the North Sea (#1 - #6), eastern (#7) and western (#8) English Channel. The regression lines indicate the extrapolation to the number of fertilized eggs at t=0.

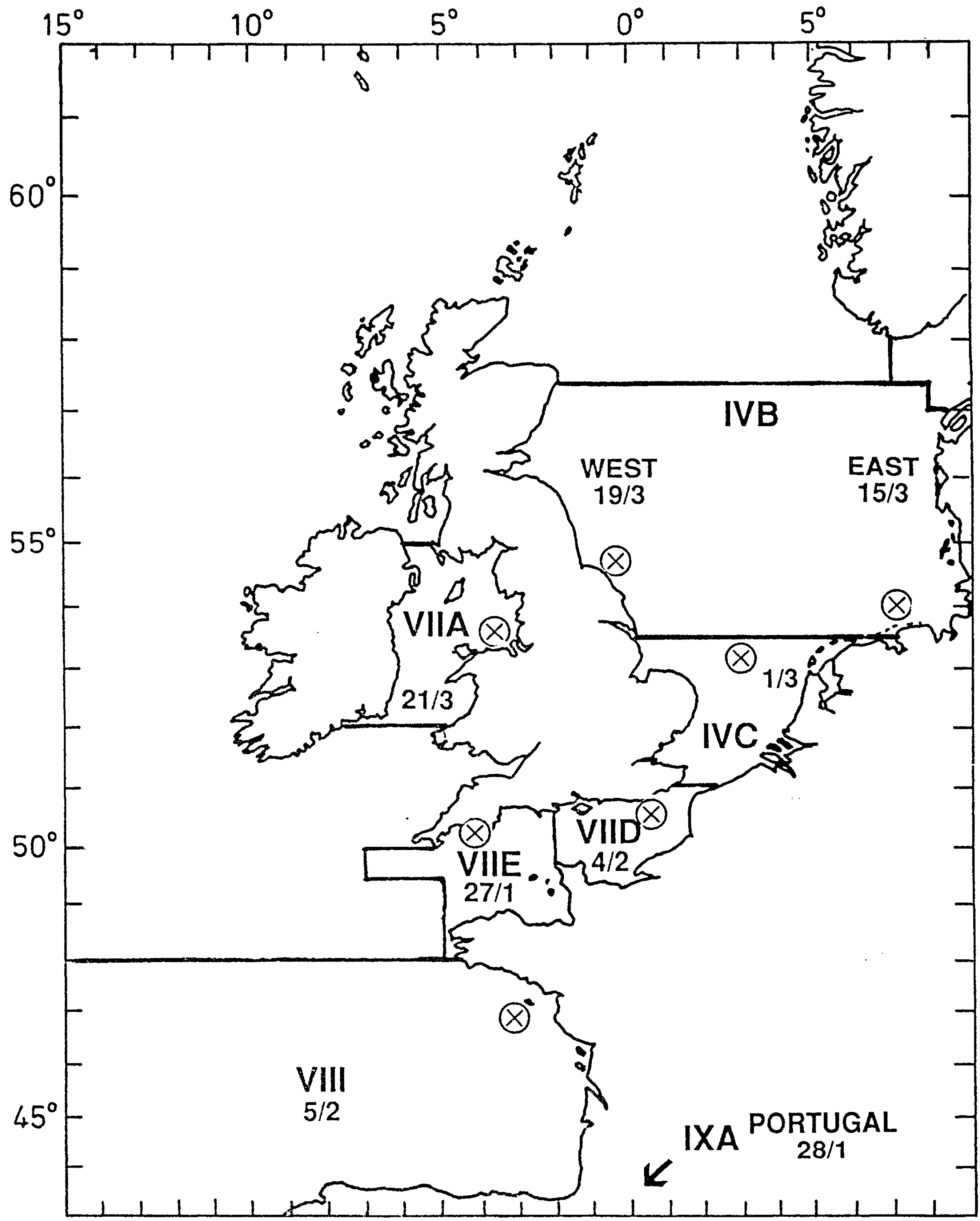
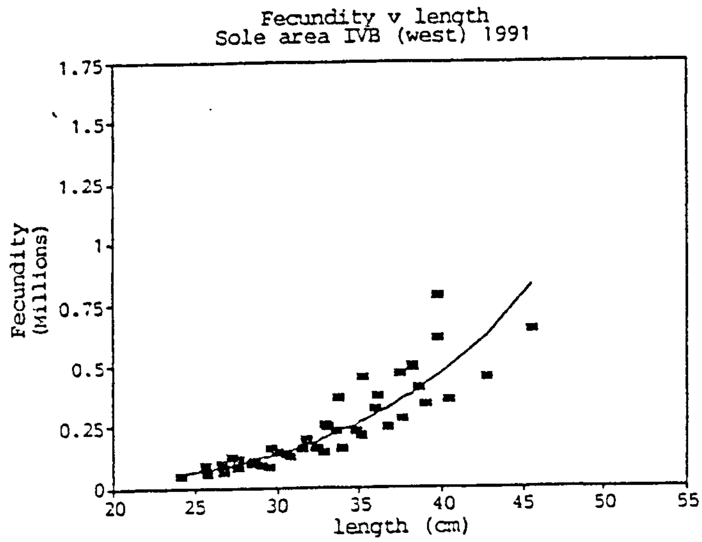
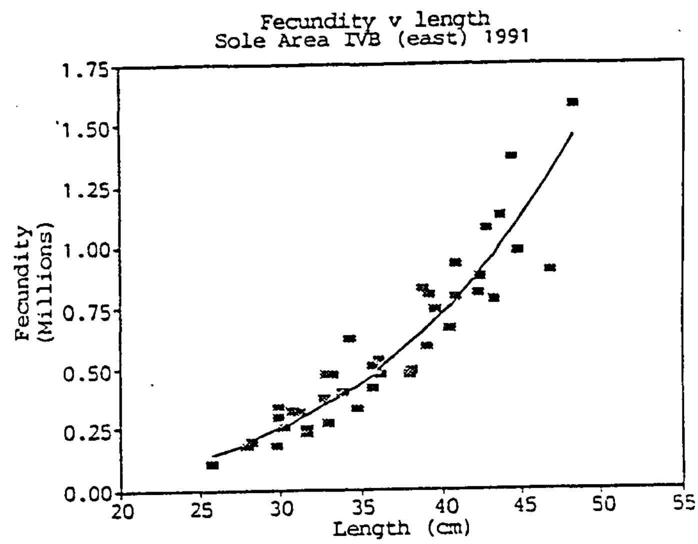


Figure 4.1. Map with locations and dates of fecundity samples collected in 1991.

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



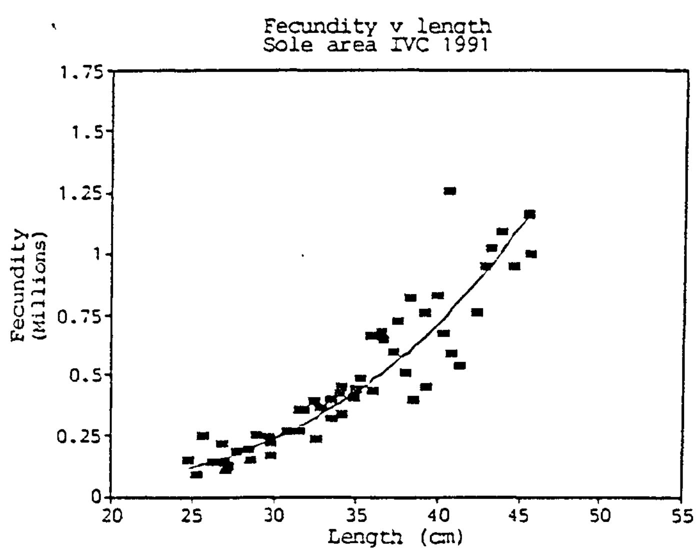


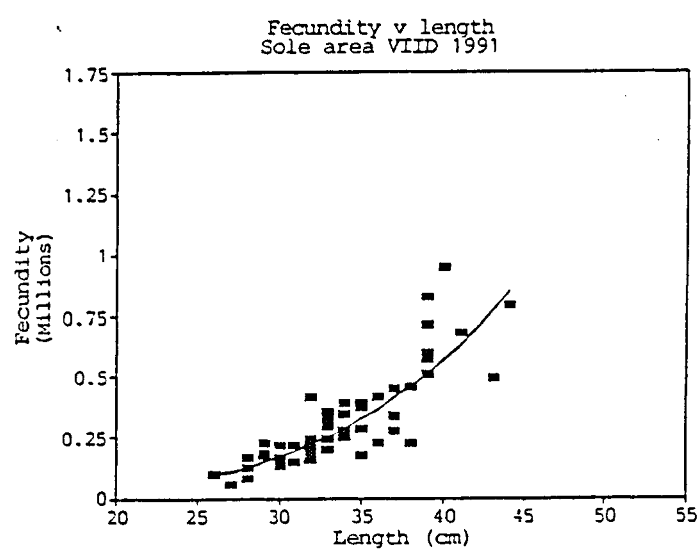
Regression Output:

Constant		-2.74951
Std Err of Y Est		0.254041
R Squared		0.875493
No. of Observations		45
Degrees of Freedom		43
X Coefficient(s)	4.285124	
Std Err of Coef.	0.246433	

Regression Output:

Constant		-0.29856
Std Err of Y Est		0.20172
R Squared		0.896726
No. of Observations		40
Degrees of Freedom		38
X Coefficient(s)	3.740706	
Std Err of Coef.	0.205934	





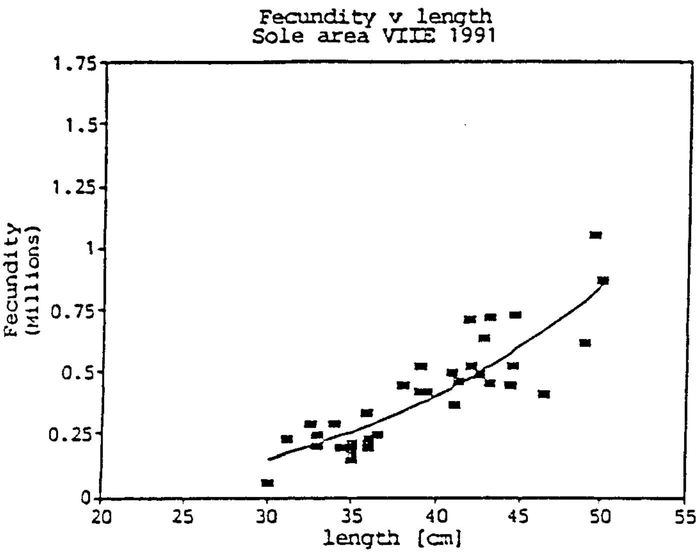
Regression Output:

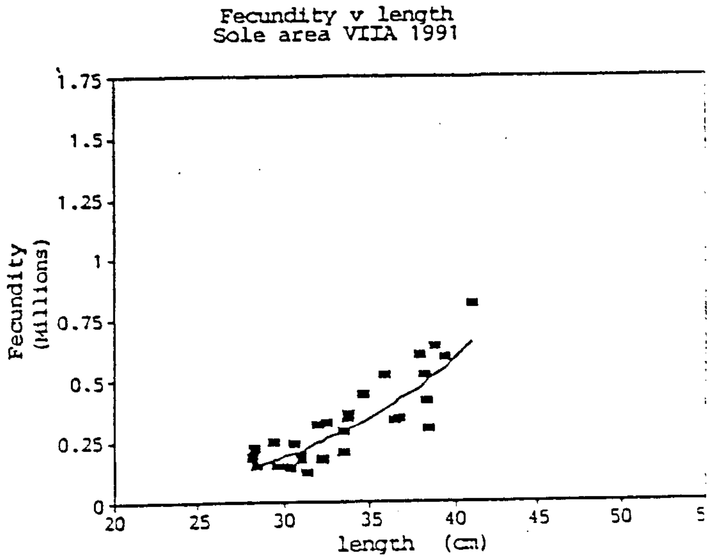
Constant		-0.56167
Std Err of Y Est		0.246092
R Squared		0.878738
No. of Observations		55
Degrees of Freedom		53
X Coefficient(s)	3.806479	
Std Err of Coef.	0.194231	

Regression Output:

Constant		-2.12695
Std Err of Y Est		0.307126
R Squared		0.758522
No. of Observations		49
Degrees of Freedom		47
X Coefficient(s)	4.169849	
Std Err of Coef.	0.343184	

Figure 4.1.1. continued.



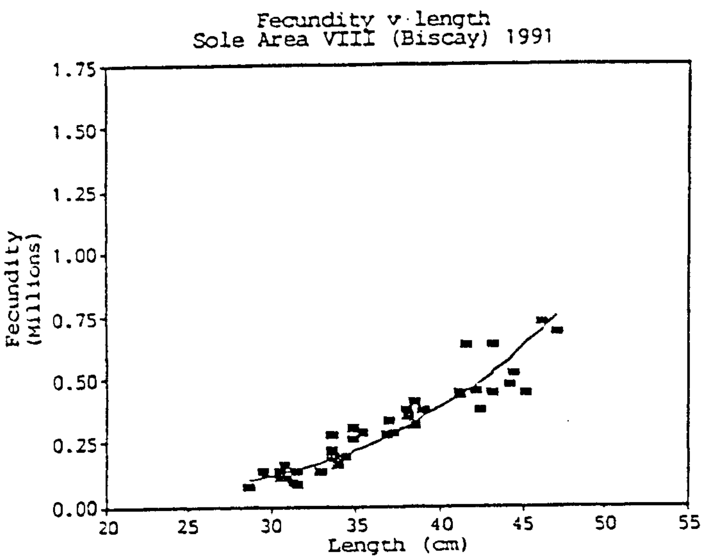


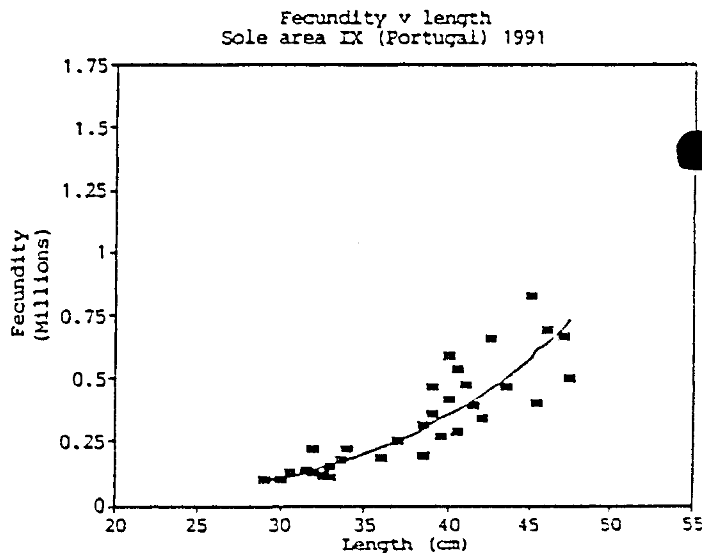
Regression Output:

Constant		0.598738
Std Err of Y Est		0.259669
R Squared		0.741361
No. of Observations		33
Degrees of Freedom		31
R=		0.861023
X Coefficient(s)	3.336464	
Std Err of Coef.	0.353946	

Regression Output:

Constant		-1.3122
Std Err of Y Est		0.277714
R Squared		0.719691
No. of Observations		29
Degrees of Freedom		27
X Coefficient(s)	3.953061	
Std Err of Coef.	0.474785	





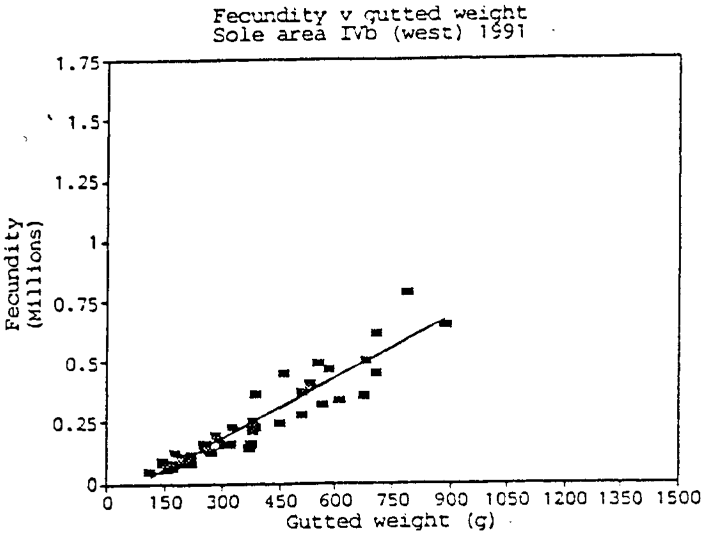
Regression Output:

Constant		-2.52197
Std Err of Y Est		0.218238
R Squared		0.879268
No. of Observations		39
Degrees of Freedom		37
X Coefficient(s)	4.167576	
Std Err of Coef.	0.253883	

Regression Output:

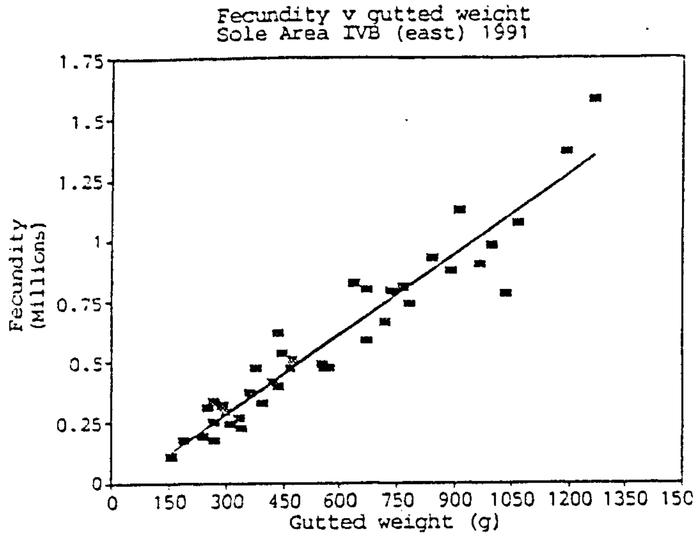
Constant		-2.77613
Std Err of Y Est		0.2638
R Squared		0.843074
No. of Observations		33
Degrees of Freedom		31
X Coefficient(s)	4.215781	
Std Err of Coef.	0.326672	

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



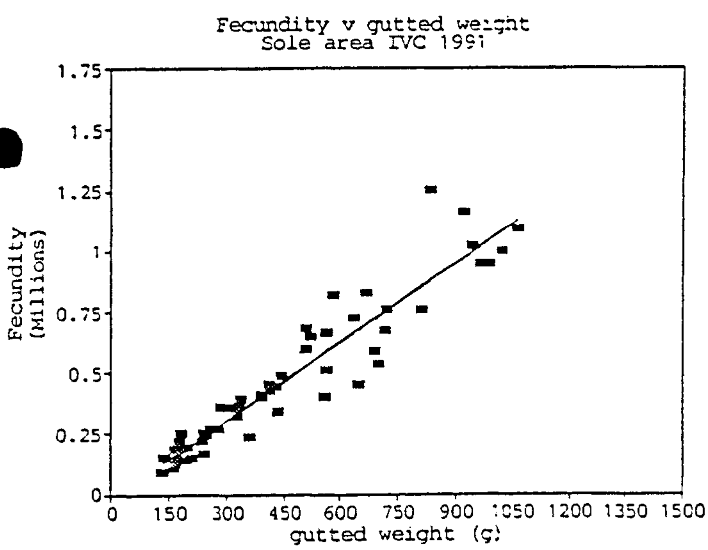
Regression Output:

Constant		-69502.8
Std Err of Y Est		63998.25
R Squared		0.872772
No. of Observations		45
Degrees of Freedom		43
X Coefficient(s)	838.3259	
Std Err of Coef.	48.81112	



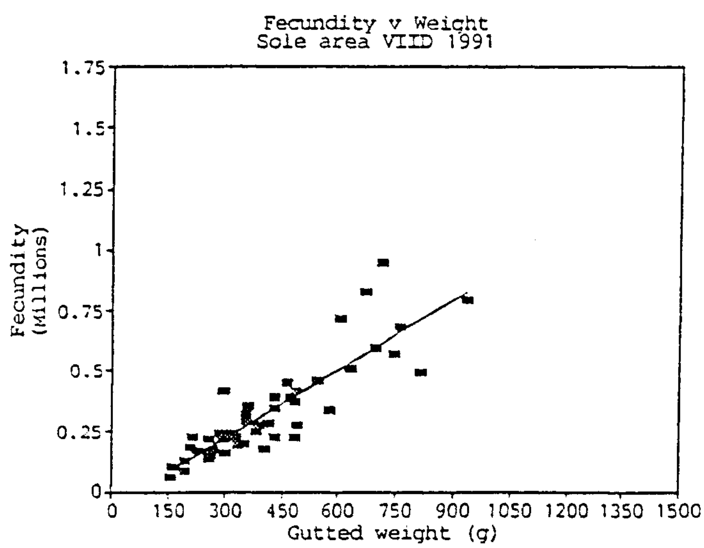
Regression Output:

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 Err of Coef.	54.93162	



Regression Output:

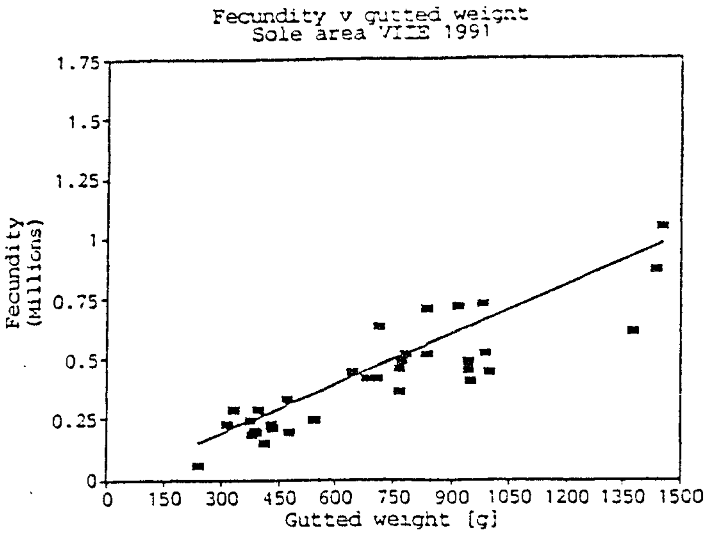
Constant		-23694.7
Std Err of Y Est		101527.4
R Squared		0.890662
No. of Observations		55
Degrees of Freedom		53
X Coefficient(s)	1078.681	
Std Err of Coef.	51.91403	



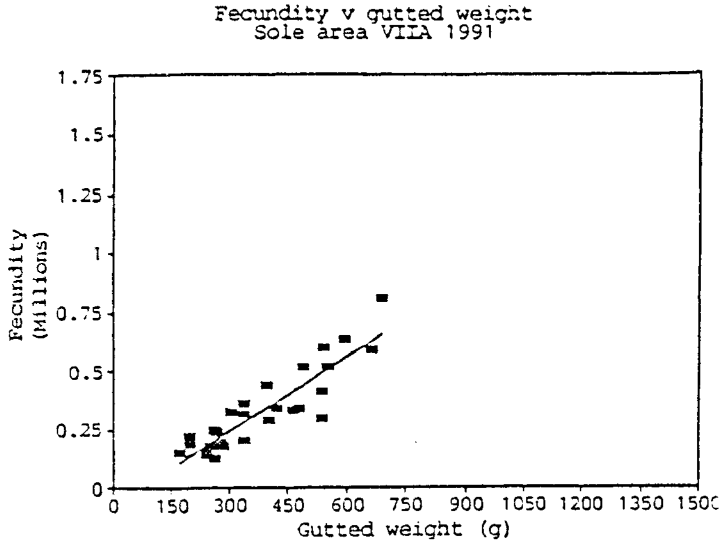
Regression Output:

Constant		-64831.4
Std Err of Y Est		99789.07
R Squared		0.766266
No. of Observations		49
Degrees of Freedom		47
X Coefficient(s)	956.2554	
Std Err of Coef.	77.03653	

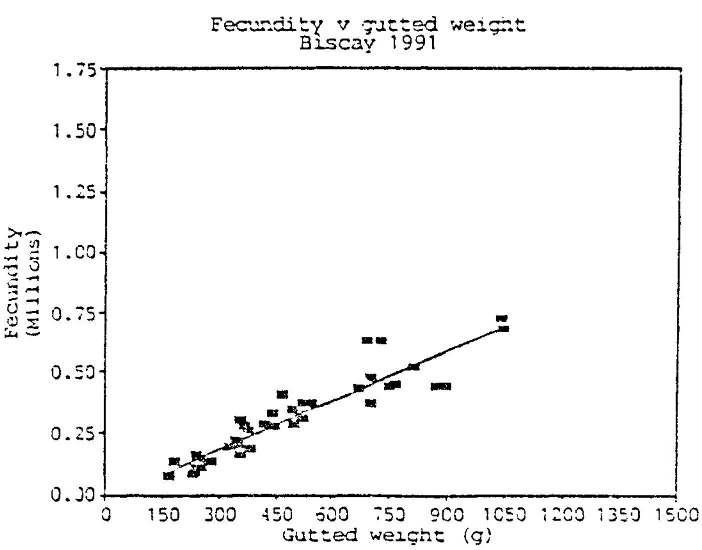
Figure 4.1.2. continued.



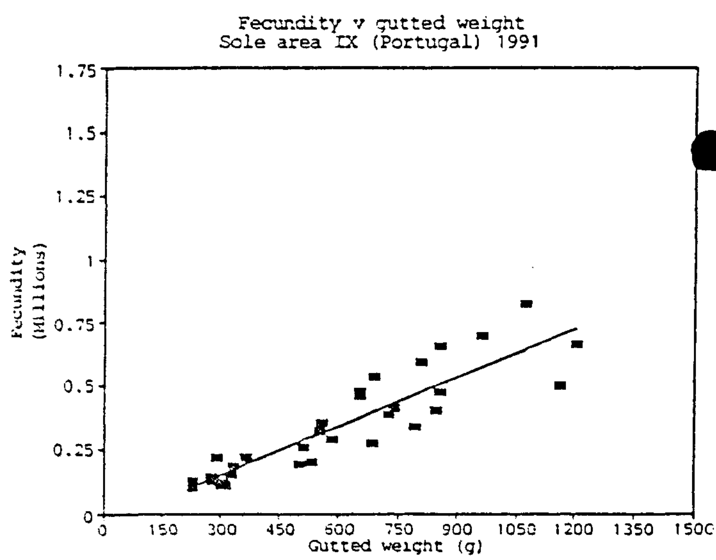
Regression Output:		
Constant		-15578.9
Std Err of Y Est		110693.4
R Squared		0.74564
No. of Observations		33
Degrees of Freedom		31
R=		0.863504
X Coefficient(s)	685.2224	
Std Err of Coef.	71.88048	



Regression Output:		
Constant		-73382
Std Err of Y Est		78587.76
R Squared		0.804481
No. of Observations		29
Degrees of Freedom		27
R		0.896929
X Coefficient(s)	1056.752	
Std Err of Coef.	100.2599	

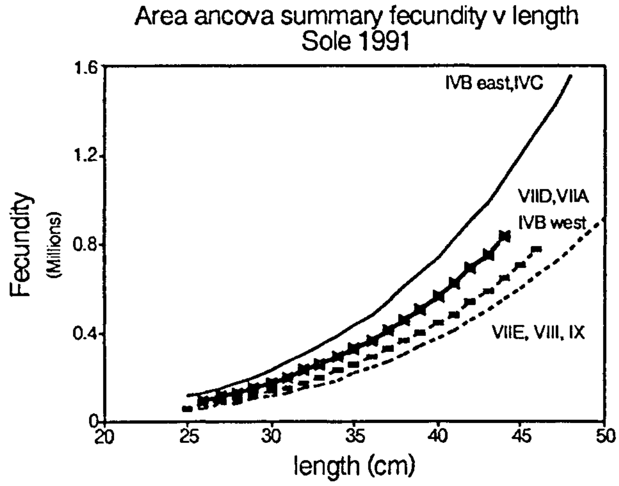


Regression Output:		
Constant		-19964.6
Std Err of Y Est		65131.27
R Squared		0.863994
No. of Observations		39
Degrees of Freedom		37
X Coefficient(s)	673.726	
Std Err of Coef.	43.94453	

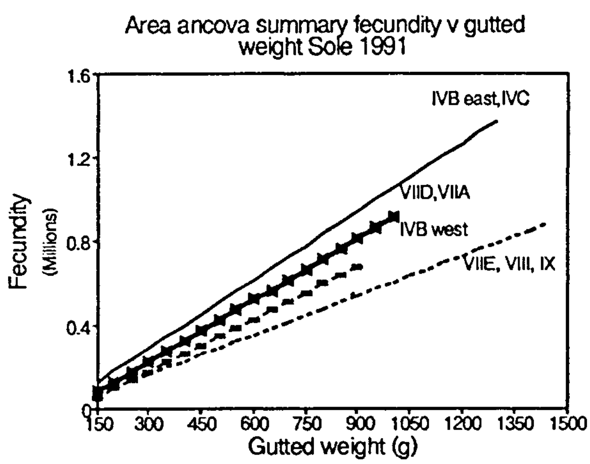


Regression Output:		
Constant		-48361
Std Err of Y Est		88399.39
R Squared		0.815674
No. of Observations		33
Degrees of Freedom		31
X Coefficient(s)	645.9096	
Std Err of Coef.	55.1476	

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.



AREA	Predicted fecundity at 37 cm	Regression of Loge transformed data slope	constant		Years 88-91 combined 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			



AREA	Regression data slope	constant		Years 88-91 combined Slope	constant
IVB (east) & IVC	1084	-30068			
VIIA & VIID	975.5	-61527	VIID only	1.176	5.619
IVB (west)	838.3	69503		1.323	4.495
VIIE, VIII, & IX	626.1	-17683		loge transformed dat	

Figure 4.1.4. Annual differences in the fecundity - body size relationship in the western North Sea (IVb west)

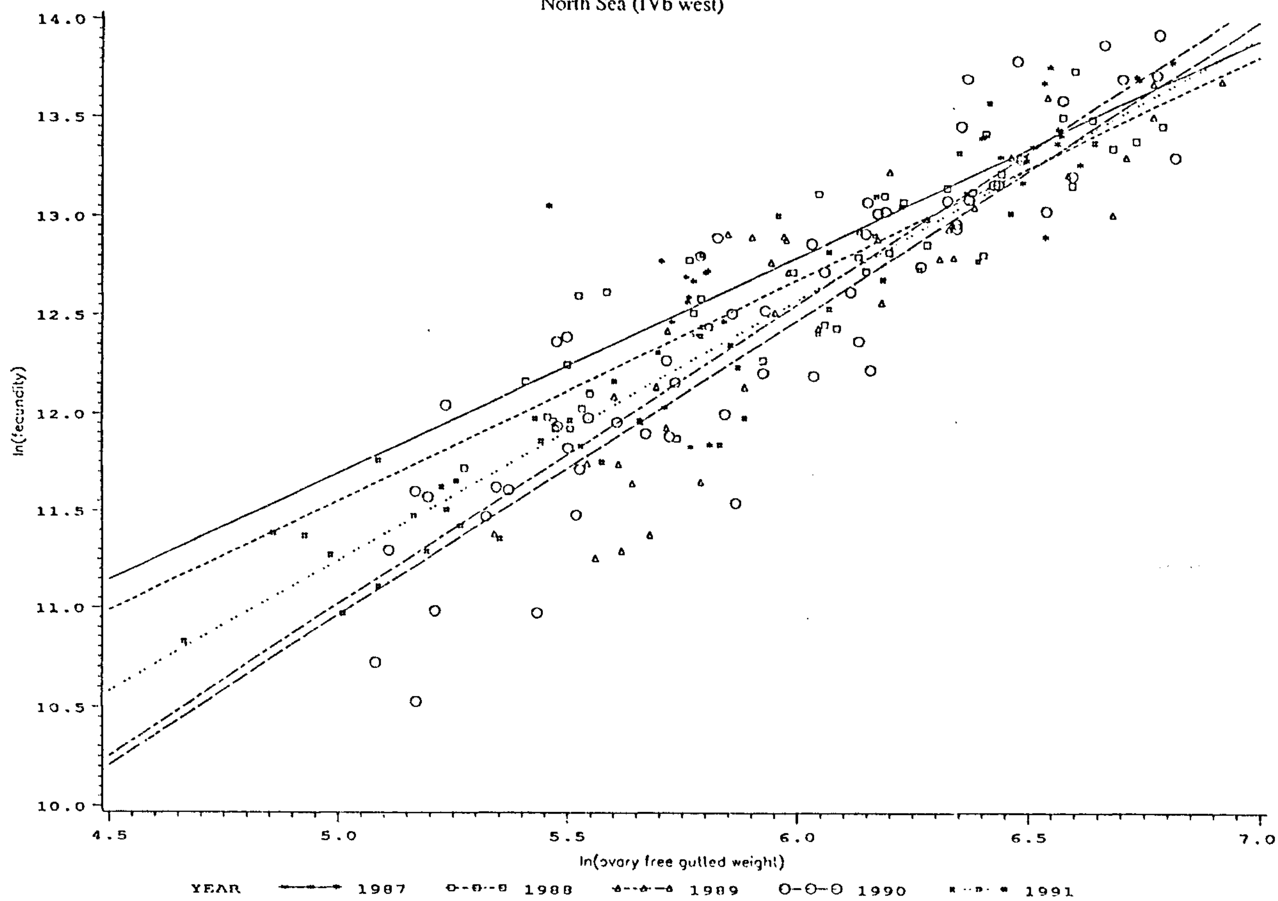


Figure 4.1 5. Annual differences in the fecundity - body size relationship in the eastern English Channel (VIId)

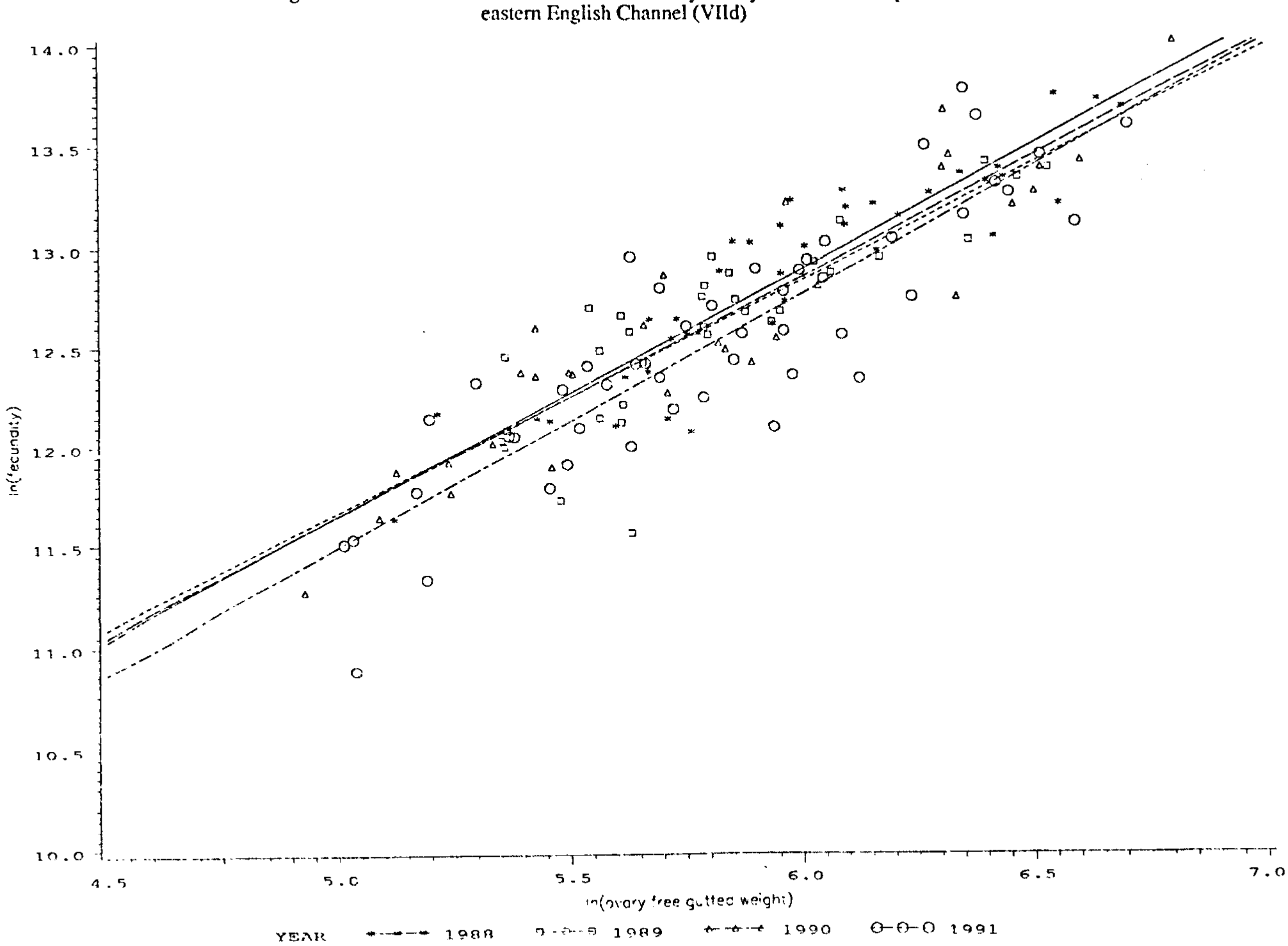


Figure 4.2.1. Frequency distributions of oocytes in the range of 150-450 µm of female sole which contained 95%-55% of their prespawning stock of vitellogenic oocytes.

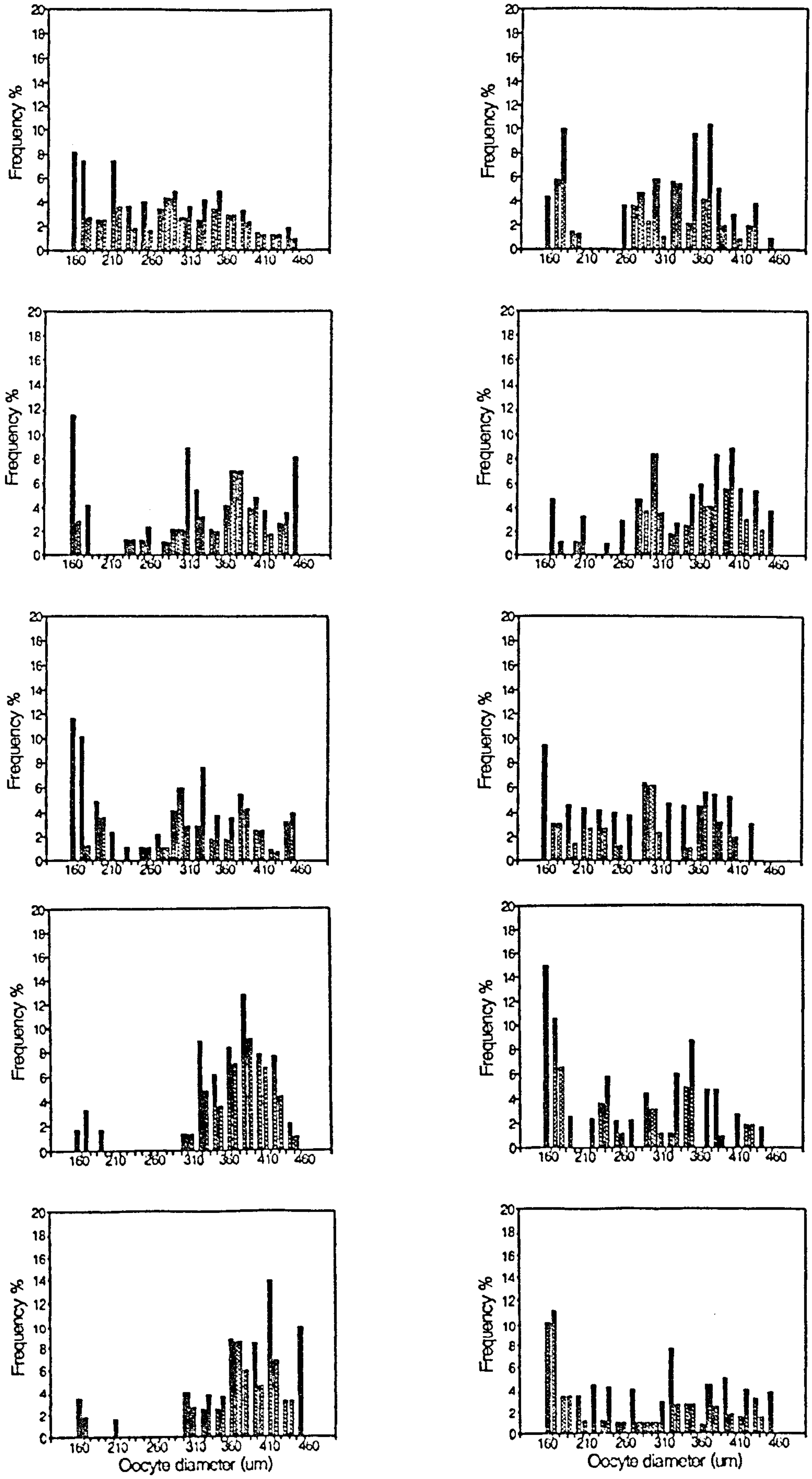
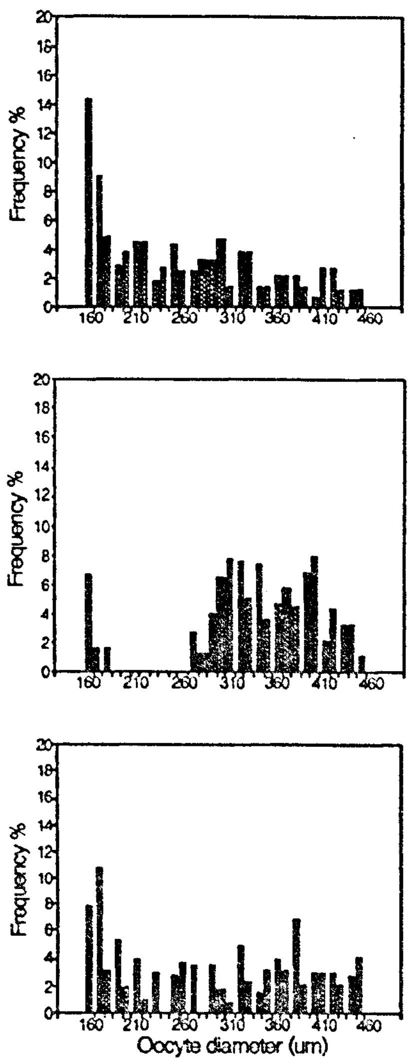
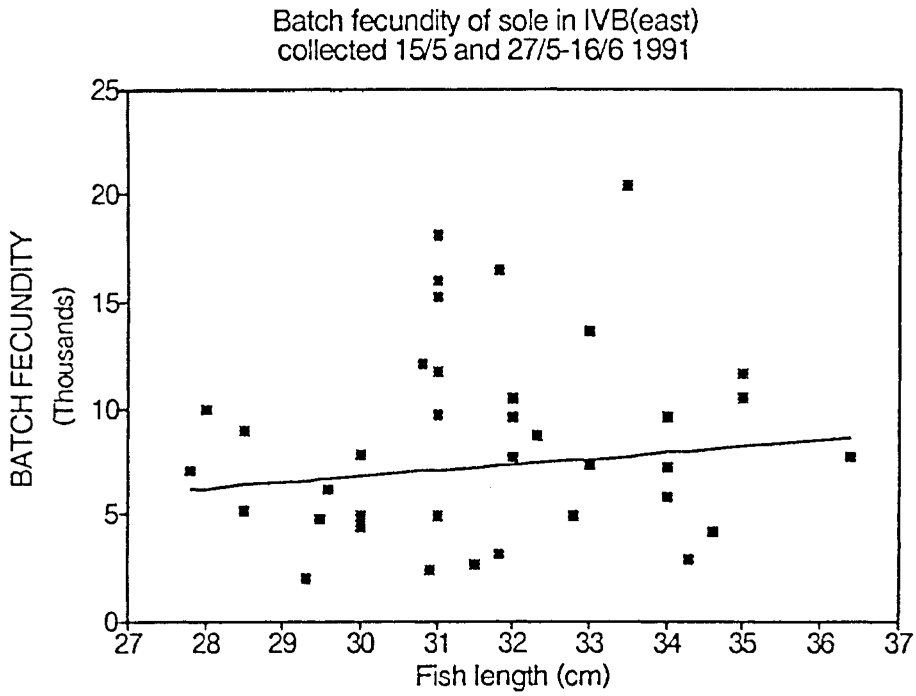


Figure 4.2.2. Frequency distributions of oocytes in the range of 150-450 μm of female sole which contained 30% of their prespawning stock of vitellogenic oocytes.



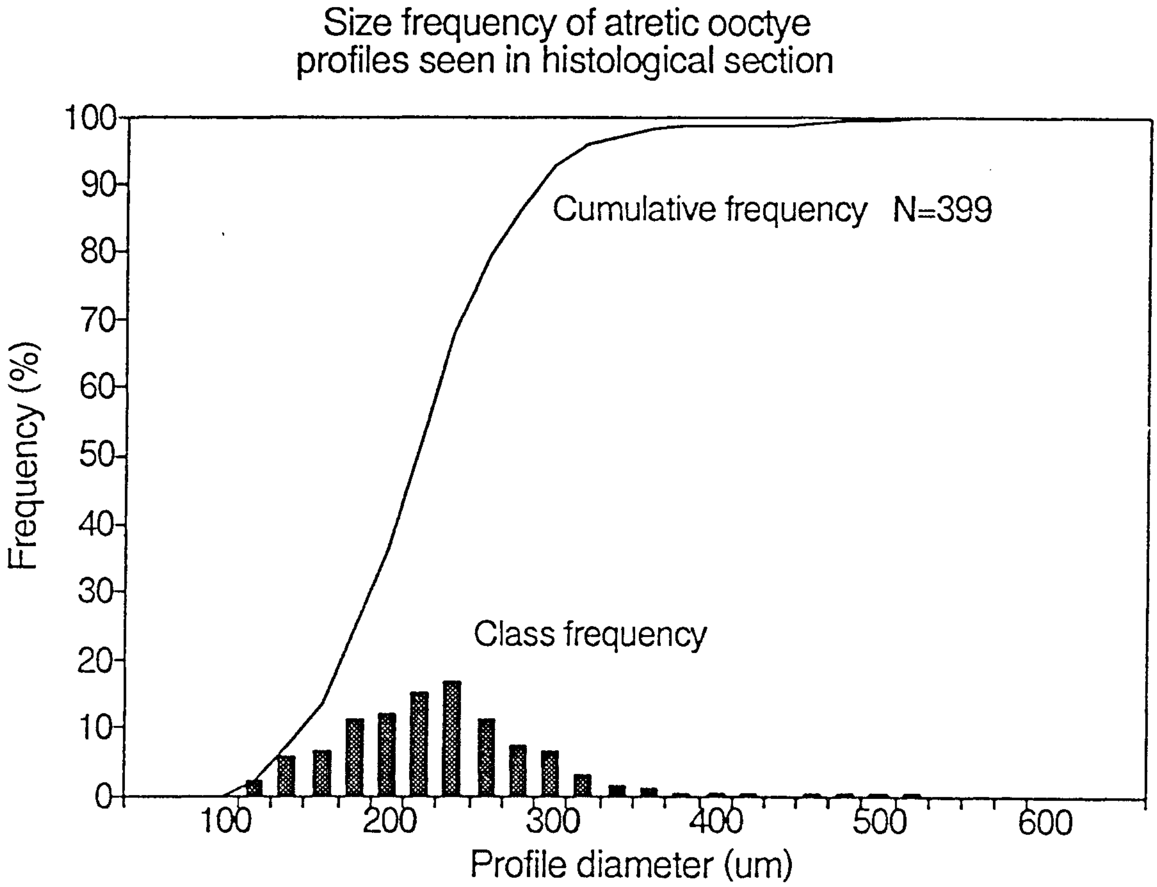


Regression Output:			
Constant	4.59959		
Std Err of Y Est	0.59505		
R Squared	0.019237	R=	0.138698
No. of Observations	38		
Degrees of Freedom	36		

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.



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

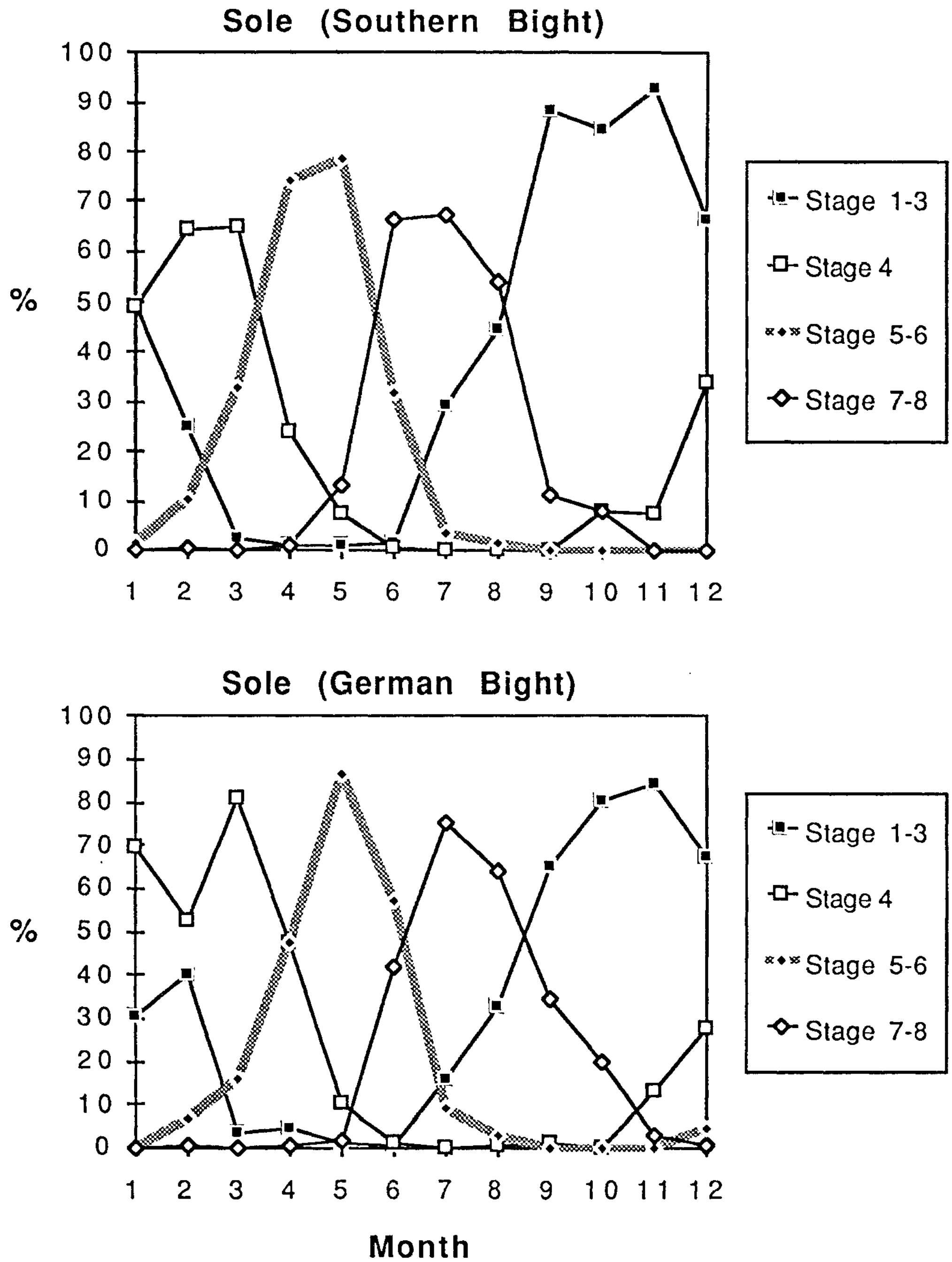


Figure 4.4.1. Frequency of maturity stages of female sole by month in the Southern Bight (above) and German Bight (below). Maturity stage 5-6 represents spawning females of age group 5+. Data: Dutch market sampling programme 1970-1979.

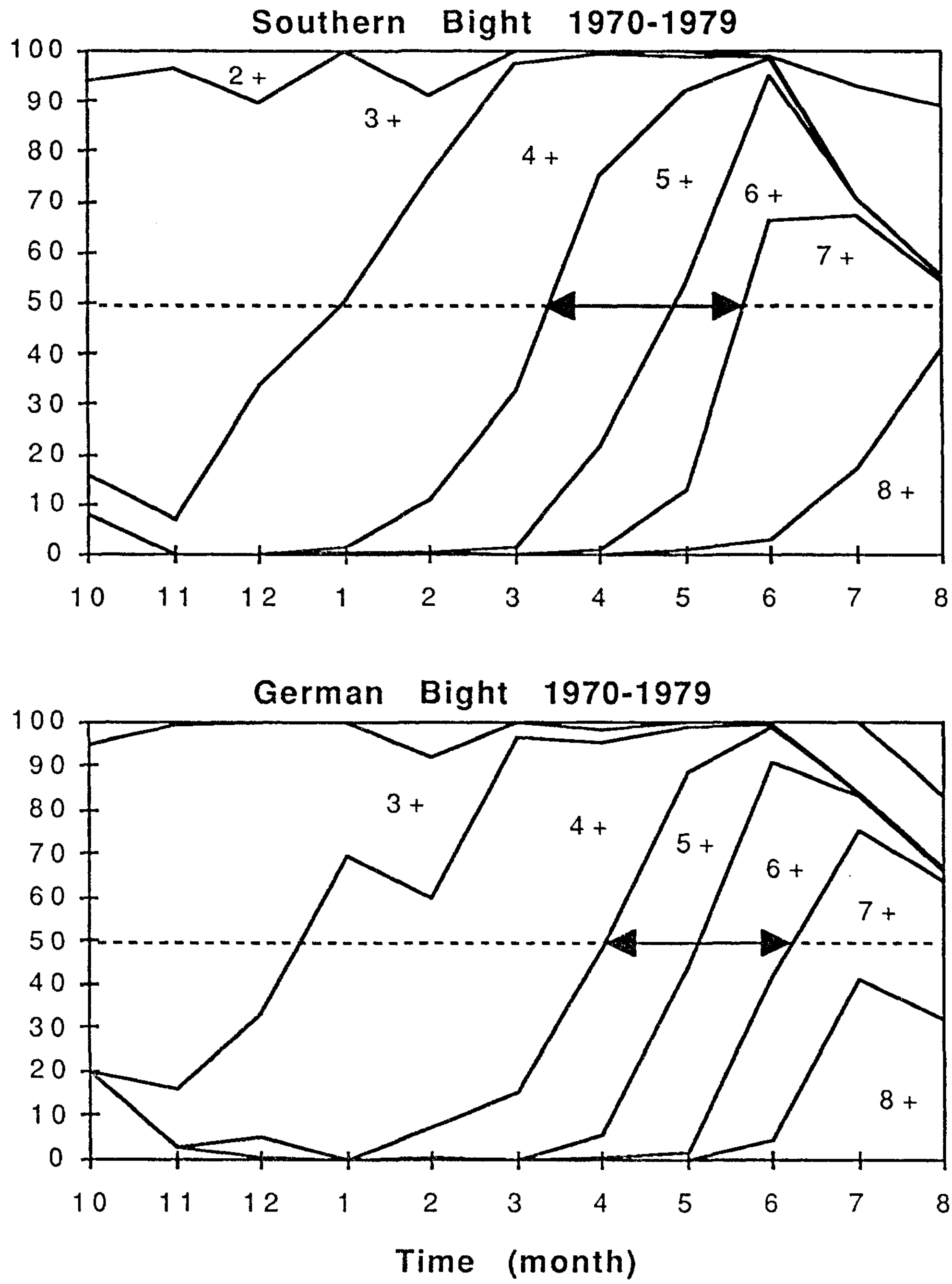


Figure 4.4.2. Cumulative frequency of maturity stages of female sole by month in the Southern Bight (above) and German Bight (below). Data of age group 5+ females from Dutch market sampling programme 1970-1979.

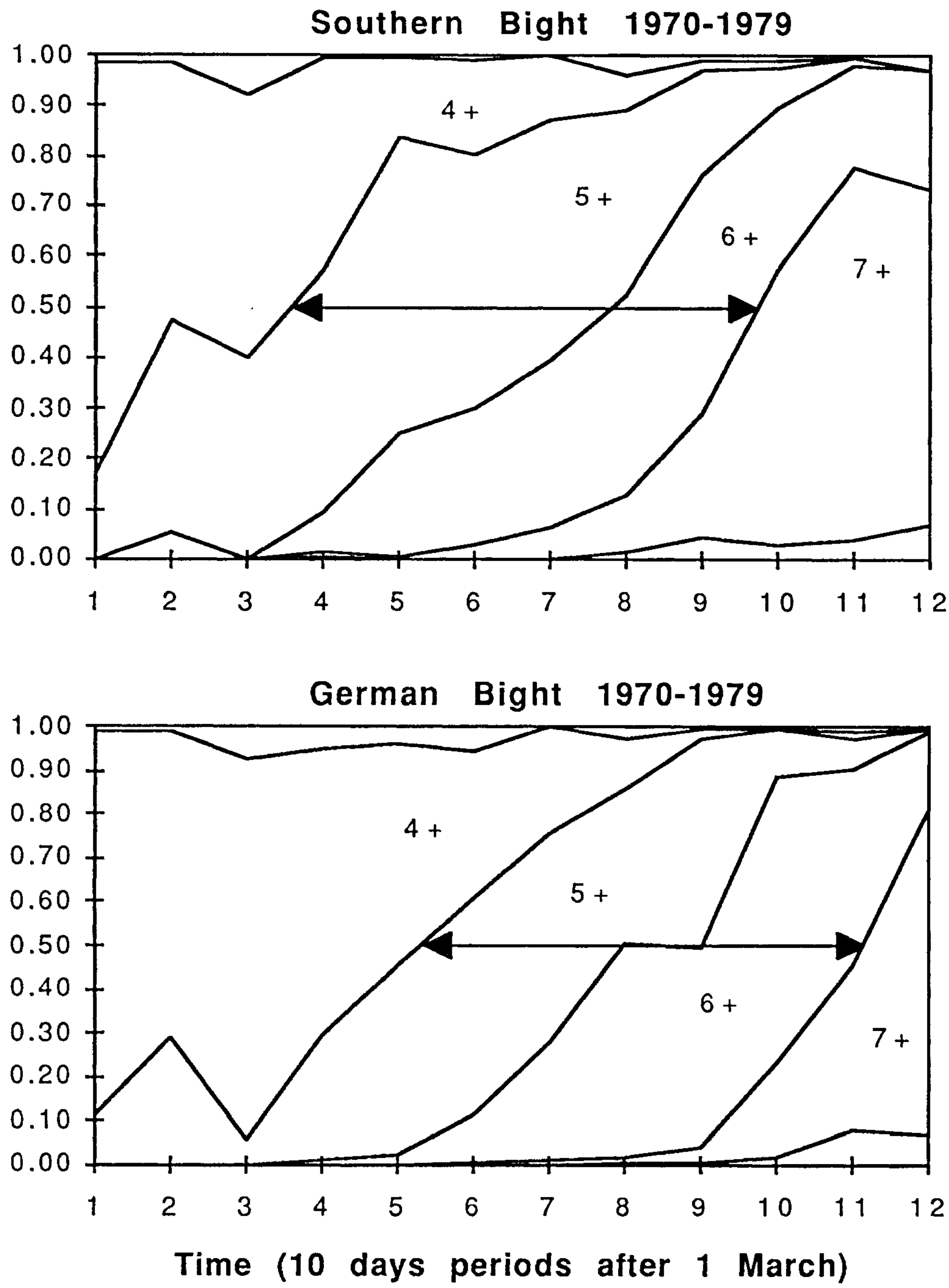


Figure 4.4.3. Cumulative frequency of maturity stages of female sole by 10-days period after 1 March in the Southern Bight (above) and German Bight (below). Data of age group 5+ females from Dutch market sampling programme 1970-1979.

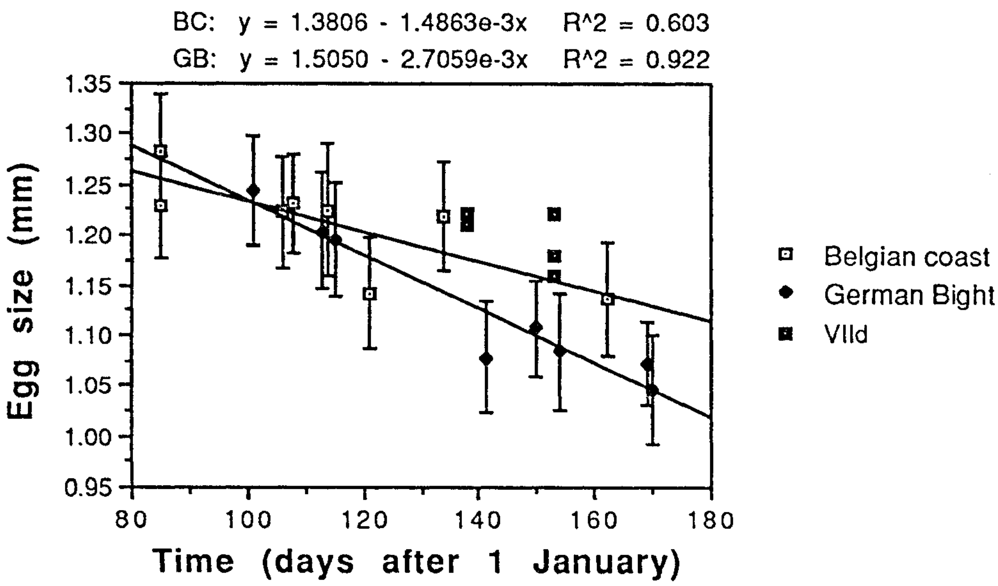
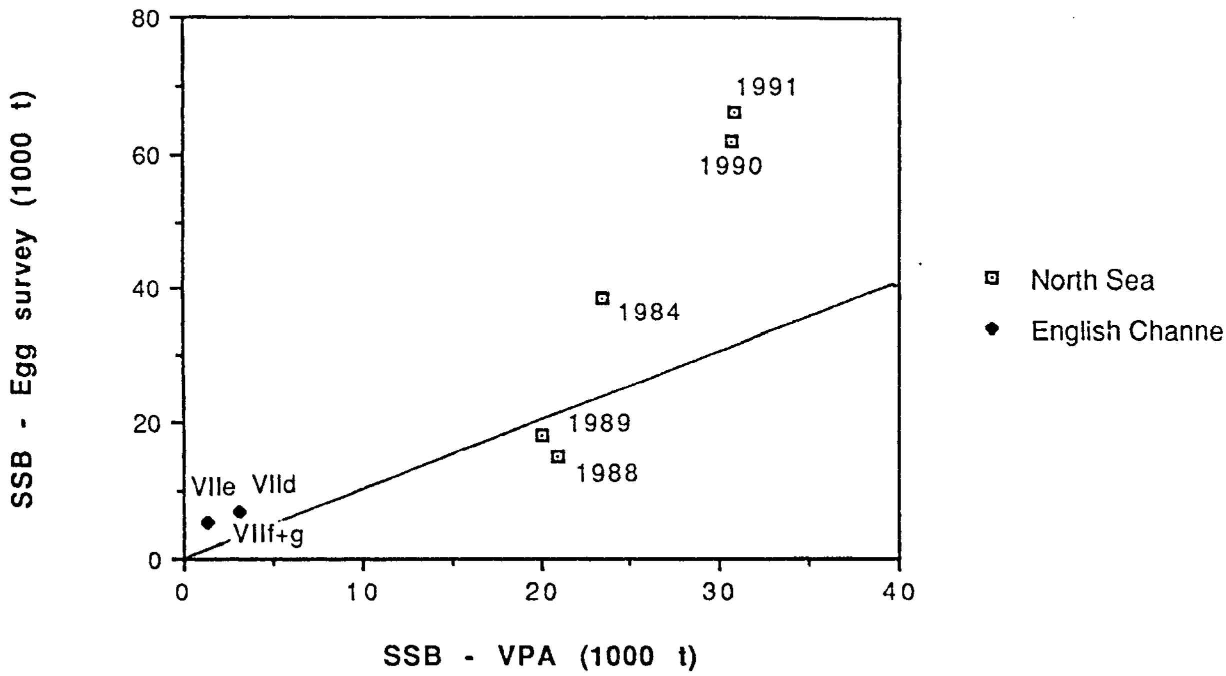


Figure 4.5.1. Mean egg size and its standard deviation against time of the year (days after 1 January) of sole eggs collected in the inner German Bight, along the Belgian coast and on the UK coast of VIId during the egg surveys between 1988 and 1991.



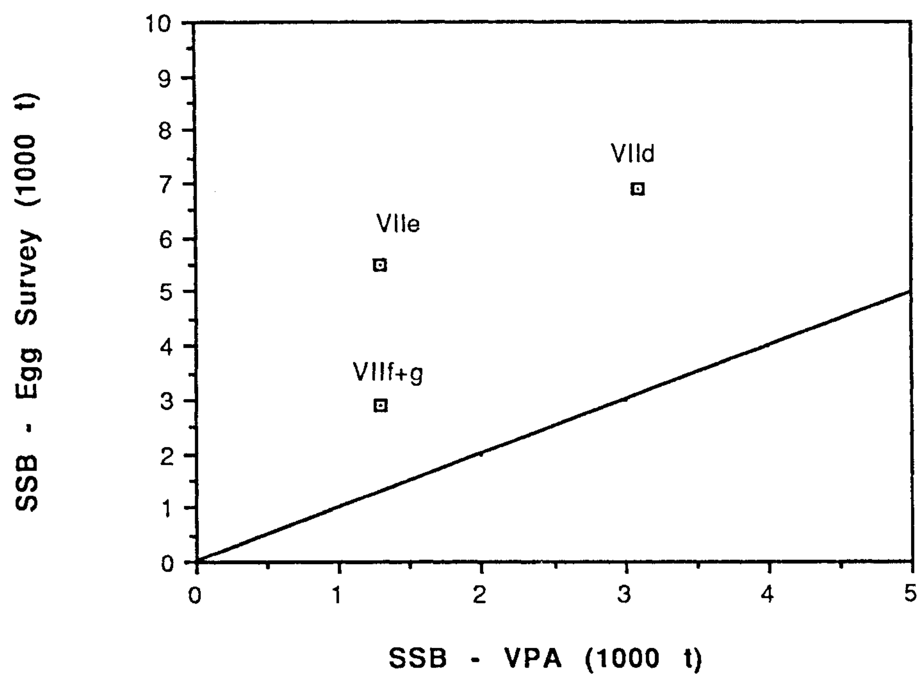


Figure 6.1. Scatter plot of the SSB estimate (1000 t) obtained by VPA and egg surveys (present study and Horwood, 1992)