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Exploration of the Sea

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**REPORT OF THE AD HOC WORKING GROUP ON
THE 1984 AND 1985 SOLE (SOLEA SOLEA L.) EGG SURVEYS**

Lowestoft, 4 - 7 February 1986

This document is a report of a Working Group of the International Council for the Exploration of the Sea and does not necessarily represent the views of the Council. Therefore, it should not be quoted without consultation with the General Secretary.

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REPORT OF THE AD HOC WORKING GROUP ON
THE 1984 AND 1985 SOLE EGG SURVEYS

1. INTRODUCTION

1.1 Participants

The ICES Ad hoc Working Group on the 1984 and 1985 Sole Egg Surveys met at Lowestoft from 4-7 February 1986 with the following participants:

F van Beek	Netherlands
R de Clerck	Belgium
R Houghton (Chairman)	United Kingdom
R Millner	"
J Nichols	"
J G Pope	"
K Stokes	"
B Thompson	"
A Thompson	"
W Weber	Fed. Rep. Germany
L Woolner	United Kingdom

Several other Lowestoft staff assisted with the analysis or participated in discussions - these were J. Riley, M. Nicholson, S. Stevens, P. Large, J. Barry and R. Ayers.

1.2 Terms of Reference

At the 1985 Statutory Meeting, it was decided (C. Res. 1985/2:4) that:

"An ad hoc meeting of the participants of the 1984 and 1985 Sole Egg Survey (Convener: Mr R G Houghton) will take place in Lowestoft (UK), 4-7 February 1986 in order to prepare a report of the results

on densities and distribution of sole eggs in the North Sea and eastern English Channel and to comment on future work."

1.3 Background to the survey

A feasibility study was proposed in 1982 and prepared at a meeting in Lowestoft on 18-21 January 1983 (Anon., 1983). The survey was planned at a further meeting in Lowestoft on 5-7 December 1983 (Anon., 1984). The latter report contains details of the sampling design for the plankton survey and also for the collection of fecundity samples.

Four surveys were planned to take place during the 1984 spawning season. These were designed to cover the expected spawning in the North Sea and eastern English Channel in space and time. In the event, certain difficulties were experienced in collecting plankton samples in each of the four surveys. Large sections of the grid were omitted from surveys 3 and 4 as a result of a problem on one of the research ships. Consequently, it was agreed that sampling should also take place during 1985 at times corresponding to surveys 3 and 4 and in such positions so as to cover the omitted parts of the grid in 1984 (the 'large gaps') and, in addition, to re-sample selected areas which were sampled in 1984 (the 'overlaps').

1.4 Objectives of the survey

The original objectives of the survey (Anon., 1983) were as follows:

- (a) to describe the distribution of sole spawning grounds and the time of spawning in different parts of the North Sea;
- (b) to determine egg mortality rates;
- (c) to estimate the total egg production and hence the female spawning stock biomass using suitable estimates of fecundity.

The present group felt that, despite the difficiencies in the data, it was still worth attempting to achieve these objectives although, of course, the accuracy with which objective (c) could be achieved would be diminished in view of the 'patching' which would have to take place between the 1984 and 1985 surveys. The surveys provide unique and valuable information on the spawning of sole in the North Sea, which the group agreed should be fully explored and explained as a basis for future work.

2. PLANKTON SAMPLING - DESCRIPTION AND METHODS

2.1 Plankton surveys

The plankton sampling and identification were carried out by Belgium (Rijksstation voor Zeevisserij, Oostende), Germany (Institut für Küsten-und Binnenfischerei, Cuxhaven; Institut für Meereskunde an der Universität Kiel), the Netherlands (Rijksinstituut voor Visserijonderzoek, IJmuiden) and the United Kingdom (Fisheries Laboratory, Lowestoft). The allocation of sample position to each nation is described in Anon. (1984) and this plan was largely adhered to.

Fifteen different vessels (including 5 commercial vessels) were employed on 35 separate cruise. In 1984, 1156 samples were obtained during 154 days at sea. In 1985 a further 261 samples were collected in 39 days at sea. Figure 2.1.1 identifies the timing of each cruise in relation to the survey periods asked for by the planning group and shows the allocation of cruises to each survey.

In view of changes in the timing of some cruises in relation to the planned survey times, it was necessary to decide on the allocation of these cruises to the 4 main surveys. The bulk of the sampling took place during the planned periods but some sampling, particularly in the Waddensee and Scheldt Estuary in surveys 1 and 2, took place 1 or 2 weeks late. The surveys were, therefore, not as synoptic as had been hoped for. Figure 2.1.2 illustrates the distribution of sampling in relation to date for 1984.

The positions of sampling are shown in Figure 2.1.3. As recommended by the planning group, special efforts were made to obtain samples from depths of less than 10 m. In 1984, 108 samples (9%) were obtained from depths of less than 10 m.

The charts of station positions for 1984 illustrate the main problem encountered in the analysis of the survey as a whole - surveys 3 and 4

were to some extent incomplete in that samples were not obtained from areas in the centre of the main grid. These omissions are subsequently referred to as 'large gaps'. 'Small gaps' also occurred in isolated sub-rectangles, particularly in inshore areas. Solutions to the problem of filling the gaps with estimates of production are described in section 3.

2.2 Sampling methods

The plankton sampling equipment used on the surveys were modified Gulf III samplers (Gehring, 1952) of 50 cm internal diameter with a 19/20 cm diameter conical nosecone. Three versions of this equipment were used, as follows:

United Kingdom : MG 82

Netherlands and Belgium : Torpedo/DG III

Germany : Nackthai

The MG82 and Torpedo/DGIII samplers have both been calibrated in a circulating water channel using the method described by Harding and Arnold (1971). The results of those calibrations given by Nichols (1982) and Wood and Nichols (1983) are summarised in the table below.

Sampler	Volume accepted in litres per second at 5 knots		
	Measured Vol.	Theoretical Vol.	Sampler efficiency %
UK/MG82 (20 cm conical nose cone)	75.3	82.1	92
Neth/Belg. Torpedo/DGIII (19 cm conical nose cone)	65.8	73.5	86

The German Nackthai net was calibrated in a wind tunnel and an efficiency of 100% for their 20 cm diameter nose cone was observed (Schoëfer, pers. comm.). For the standard UK sampler the electronic flowmeter was calibrated in situ during the flume trials, providing a direct relationship between revolutions and volume filtered irrespective of clogging. For the other samplers and the UK sampler used with a mechanical flowmeter on some inshore surveys, calibration of the flowmeter was done at sea. Briefly the method used was to obtain a relationship between revolutions per second and speed over the range of potential towing speeds (i.e. 4-6 knots) in free flow (i.e. without a net). This free flow calibration was then be compared with observed revolutions per second on each haul to provide a measure of the reduction in flow caused by the presence of the net and clogging. This factor was then applied to the measured volume accepted (table above) thus taking into account the inherent inefficiency of the nose cones. The methods of free flow calibration and measurement of ships speed are described in detail in the Manual for the International Herring Larvae Surveys (Anon., 1985).

Each sample consisted of a (single or multiple) double oblique haul to as close to the sea-bed as possible at a standard towing speed of 5 knots. The mean sampled depth in 1984 was 22.0 m compared with a mean water depth of 24.3 m. The average ratio of sampled to water depth was 0.90. 93% of samples had a ratio greater than 0.8 and in 62% the ratio was greater than 0.9. Samples were taken throughout the 24 hours of the day and night.

A range of plankton net mesh sizes were used. They varied according to the occurrence or likelihood of clogging by algae and what was available for the particular type of net. The proportion of samples in 1984 which employed the different mesh sizes were as follows:

Mesh size (μm)	Number of samples	%
270	310	26.8
300	132	11.4
420	117	10.1
480	18	1.6
500	579	50.1
Total	1156	

The planning group (Anon., 1984) recommended that each sample should be the result of filtering at least 50 m^3 of sea-water. In fact, during 1984 431 of the samples (23.8%) filtered less than 50 m^3 . The mean volume filtered was 55.1 m^3 (± 42.2 , 2 SD). In shallow depths it was impossible to filter the required volume in the restricted areas available due to the sub-rectangle limits and the bathymetry.

Clogging by Phaeocystis in inshore areas during May and June was occasionally experienced but it did not cause the expected flow to fall below the 50% threshold recommended by the planning group. Only small (< 10%) reductions in expected flow were experienced.

All samples, after being carefully washed down on board into a collecting bag, were fixed in 4% buffered formaldehyde in fresh or distilled water. All samples were sorted by the countries collecting them. Sole eggs were identified according to descriptions in Russell (1976) and Nichols (1976) and staged using Riley's (1974) criteria.

Precautions were taken to ensure that the identification and staging of sole eggs in the samples were consistent between the 5 laboratories participating. Photographs and descriptions were distributed; samples sorted at Cuxhaven were checked at Lowestoft prior to the 1984 survey, and training was given in 1984 at Lowestoft to the assistant working on the Belgian samples. During the meeting, 5 Cuxhaven and 5 IJmuiden

samples were checked at Lowestoft, the results from which are shown in Tables 2.2.1 and 2.2.2. Some discrepancies exist in total number of sole identified and in the staging but, overall, it was clear that a reasonable level of consistency had been achieved.

2.3 Data processing

The data for each sample were exchanged on the data form designed by the Planning Group (Table 2.3.1). All forms were sent to Lowestoft and punched twice before entry into the computer. The data were then verified through a computer program which checked the ranges and validity of selected fields as indicated in Table 2.3.2.

Listings of the data were sent to the participants who then checked that the basic data were correct.

The data were then loaded into a 'dBASE II' database on an Apricot microcomputer. Unique record numbers were added to each record as was the area (in km²) of the sub-rectangle from which the sample was taken. (The areas of sub-rectangles were measured by planimetry from Admiralty metric charts using the published shore-line as the landward boundary; this corresponds to the mean low-water spring tide level). The average of surface and bottom temperatures was then calculated and added to each record (if either was absent, the other temperature was used as the average).

The secondary, parallel database was then constructed by copying the record number from the primary database. The duration of each egg stage was added to this, calculated from the average temperatures of each station using the following formulae:

$$d_n = \exp(b_n t + a_n)$$

where d_n is the duration in days of the stage in question and t is the

average temperature. The coefficients for each stage (n) were as follows (Riley, personal communication).

Stage	a	b
1	2.0193	-0.1227
2	1.4941	-0.1530
3	2.5075	-0.1509
4	1.4106	-0.0687

The densities (no/m^2), numbers produced per m^2 per day ($\text{no}/\text{m}^2/\text{day}$) and production ($\text{no}/\text{subrectangle}/\text{day}$) of each egg stage and the larvae were then calculated and added to the secondary database using the following formulae:

$$\text{No}/\text{m}^2 = \text{count}/(\text{volume filtered}) * \text{depth}$$

$$\text{No}/\text{m}^2/\text{day} = \text{density}/\text{duration}$$

$$\text{Production} = (\text{no}/\text{m}^2/\text{day}) * \text{area}.$$

The analysis had to allow for the possibility of replicate stations having been taken within a sub-rectangle and survey, since total production per day was to be calculated as the sum of the production per day in each subrectangle. The non-replicates and replicates were identified by first sorting the primary data base on main survey, rectangle and subrectangle. Sequences of the same survey, rectangle and sub-rectangle indicated the existence of replicates. The program identified the non-replicates and replicates by the addition of an extra field to each record. Averaged replicates were calculated and added as additional records at the end of each data base; these were also uniquely identified.

Programs were written to summarise the production of each egg stage on each survey and to calculate the mean stage durations. Data were also extracted and converted to a chart format using the spreadsheet program "Supercalc 3". An example of this format is shown in Table 2.3.3. These

presentations were used to identify the small and large gaps and to calculate the extrapolated productions as well as to prepare the distribution charts.

3. DISTRIBUTION OF SOLE EGGS AND LARVAE AND THE INFLUENCE OF ENVIRONMENTAL VARIABLES ON PRODUCTION

3.1 Distribution of sole eggs

Data from surveys 1 to 4 in 1984 provide an overall picture of sole spawning in the Southern Bight from the beginning of April through to the end of June. The abundance of Stage I to IV eggs as numbers per m² for each survey (including 1985) is shown in Figures 3.1.1a to 3.1.1r.

Stage I egg abundance can be used as an indication of the existence of spawning areas and here it shows that spawning began during April in coastal waters south of 51°30'N, off the Belgian and Dutch coasts and close to the mouth of the Somme. As the season progressed, centres of spawning developed to the north in the Thames and Humber estuaries, the Wash, in the Scheldt estuary, along the Dutch coast and into the German Bight. The densities of Stage I eggs declined during June although spawning was still taking place over most of the surveyed area. Throughout the season, the distribution of sole eggs was patchy, and although they occurred over most of the Southern Bight areas, the main areas of spawning appear to have been in well-defined parts of the shallow coastal waters.

The distribution of Stages II to IV closely followed that of Stage I suggesting that the patches of sole eggs remain discrete during their development.

Sole larvae were found in a single subrectangle during Survey I and occurred in increasing numbers throughout Surveys II, III and IV. The larval distributions are shown in Figures 3.1.2 a to d. There is an indication, particularly in the German Bight, that the larvae drifted away from the spawning areas into slightly deeper water offshore.

3.2 Distribution of environmental variables

The observed temperatures for surveys 1 to 4 in 1984 are shown in Figures 3.2.1a to 3.2.1d. These are mainly surface temperatures although little vertical stratification was found in the areas surveyed when both surface and bottom temperatures were measured. The mean sea temperature observed on each survey (irrespective of the catch of sole eggs) in 1984 were as follows:

Survey	°C	n	SD
1	6.9	155	1.2
2	8.4	372	1.6
3	10.2	334	1.3
4	13.3	295	2.3

Infra-red satellite images of the survey area were obtained from the University of Dundee and interpreted initially by Dr P Holligan of Institute for Marine and Environmental Research at Plymouth. The approximate positions of the sharper thermal fronts are indicated in Figure 3.2.2a to d at times corresponding to the four main surveys. Extended clear weather occurred particularly at the end of April during Survey 2, but also as occasional days during the other Surveys.

A warm inflow into the Southern Bight occurred during March and early April at the time of Survey 1; this had a clearly defined north-western boundary with colder water along the English and continental coasts. The inflow dissipated off the Wadden Islands in a billowing structure extending approximately 100 km offshore. Warm spots could be detected extending to the north of the Rhine Delta and also in the coastal area of the German Bight. Other structures could be observed around the Dogger Bank.

By the time of Survey 2, at the end of April, the strong inflow from the Channel appeared to have diminished and the sea surface thermal

structure was dominated by warm water in inshore areas extending north from the Belgian coast and Rhine delta, in the Thames Wash and German Bight. The Flamborough front became established in the last week of April.

A much more confused thermal structure occurred in mid-May just prior to Survey 3. Inshore warm patches were again detectable off the main estuaries and deltas and large patches of warmer water dominated the central Southern Bight and the German Bight. The Flamborough front was again visible in a more northerly position.

By June at the time of Survey 4 the central patches of warm water had disappeared and there remained the inshore patches observed previously, dominated particularly by that extending north from the Rhine. Topographical features (Norfolk & Hinder Banks, for example) were reflected in the thermal images during this period, possibly at low tide suggesting that tidal movements rather than wind driven or residual drift was the main cause of water movement during June.

The majority of samples were taken within the 40 m depth contour with occasional samples in deeper water off Flamborough for example. The frequency distribution of samples in relation to water depth for 1984 is shown in Figure 3.2.3. It clearly was not possible to sample extensively in depths less than 5 m. The mean water depth was 25.1 m but ranged from 4 m to 71 m.

It was the intention to sample throughout the 24 hour period. Figure 3.2.4 shows the distribution of samples in relation to time of day for the whole of the 1984 survey. For non-replicate stations (largely excluding the inshore sampling in depths less than 10 m) were reasonably evenly distributed with a slightly greater proportion of samples taken during daylight hours. The replicate hauls, however were strongly

diurnal with the majority taken in daylight hours - mainly because the work was carried out from small day-boats.

3.3 An analysis of the effect of environmental and other variables on spawning

A Gaussian production curve for stage I sole eggs (S_1 , eggs $m^{-2}day^{-1}$) was modelled using the GLIM package by fitting a quadratic equation to $\ln(S_1 + 0.1)$. Quadratic functions were either $DAY + DAY^2$ (Julian) or $TEMPERATURE + TEMPERATURE^2$. The effects of DEPTH, LATITUDE, LONGITUDE, RECTANGLE, and the interactions LATITUDE x LONGITUDE and LATITUDE x DAY were investigated on these basic models. In models 1 and 3 (see below) the rectangles were included as 63 factors. The interaction LATITUDE x LONGITUDE allowed for an examination of effects that cannot be simply described by north-south or east-west terms. The interaction LATITUDE x DAY allowed for a latitudinal effect in the timing of the egg production.

A production curve fitted using DAY explained some of the variance, with substantially more being explained after RECTANGLE and LATITUDE x DAY were included in the model (EQ.1, Table 3.3.1).

$$\ln(S_1 + 0.1) = \mu + \alpha DAY + \beta DAY^2 + \gamma RECTANGLE + \delta LATITUDE \times LONGITUDE + \text{error} \quad (\text{EQ.1})$$

Most of this reduction occurred when RECTANGLE was added. This was expected, as this factor accounts for both geographical and environmental effects. A different model was fitted, which used LATITUDE, LONGITUDE, LATITUDE x LONGITUDE, and DEPTH as variables, instead of the factor RECTANGLE (EQ.2).

$$\ln(S_1 + 0.1) = \mu + \alpha DAY + \beta DAY^2 + \gamma LATITUDE + \delta LONGITUDE + \epsilon LATITUDE \times LONGITUDE + \zeta LATITUDE \times DAY + \eta DEPTH + \text{error} \quad (\text{EQ.2})$$

In this case the reduction in variance was almost as good (with the error MS being 1.64 as opposed to 1.46) and the model used only 7 instead of 65 degrees of freedom (Table 3.3.2). Examination of the regression coefficients of EQ.2 (Table 3.3.5) showed that egg production increased when moving from north to south, and when moving from west to east, and from deeper to shallower water (Fig. 3.3.1). The interaction LATITUDE x DAY, which explained much of the variance, showed that the timing of egg production gets later with increasing latitude. Egg production was negatively associated with depth, but no significant LATITUDE x LONGITUDE effect was found.

A production curve fitted to TEMPERATURE explained a slightly higher proportion of the variance than the model fitted to DAY (EQ.3 and compare Tables 3.3.1 and 3.3.2 with 3.3.3 and 3.3.4).

$$\ln(SI + 0.1) = \mu + \alpha \text{ TEMPERATURE} + \beta \text{ TEMPERATURE}^2 + \gamma \text{ RECTANGLE} + \delta \text{ LATITUDE} \times \text{LONGITUDE} + \text{error} \quad (\text{EQ.3})$$

It was noticeable that RECTANGLE explained a higher proportion of the variance in the fit to DAY (EQ.1) compared to this fit to TEMPERATURE; this was presumably because RECTANGLE also explained some of the TEMPERATURE effect. A good fit to egg production was obtained with the following temperature model (EQ.4 and Table 1.3.4).

$$\ln(SI + 0.1) = \mu + \alpha \text{ TEMPERATURE} + \beta \text{ TEMPERATURE}^2 + \gamma \text{ LATITUDE} + \delta \text{ LONGITUDE} + \epsilon \text{ LATITUDE} \times \text{LONGITUDE} + \zeta \text{ LATITUDE} \times \text{DAY} + \eta \text{ DEPTH} + \text{error} \quad (\text{EQ.4})$$

As with the DAY based model, there was no significant LATITUDE x LONGITUDE effect, but the other variables caused a significant reduction in variance (Table 3.3.4). The variance of the model using the separate variables was again close to that of the model using RECTANGLE (with the error MS being 1.54 as opposed to 1.44) and the number of model degrees

of freedom used was similarly only 7 instead of 65. The square of the multiple correlation coefficient (R^2) is a measure of the amount of variance explained by the model, and is included in Tables 3.3.1-4.

The results indicated that a Gaussian production curve on day or temperature described the pattern of (the logarithm of) egg production. Additional environmental variables used in the model explained the observed geographical differences in egg production, of which TEMPERATURE and LATITUDE x DAY explained the highest proportion of the variance but DEPTH was also of importance. The results suggest that of those examined, TEMPERATURE was the most important variable describing egg production. The most useful model, however, was EQ.2, since the variables were biologically meaningful and, because the independent variable was time based, the curve can be integrated to obtain an estimate of seasonal egg production. The regression coefficients and their standard errors for this model are shown in Table 3.3.5.

4. EGG MORTALITY AND PRODUCTION

4.1 Survey coverage

Coverage was near complete on surveys 1 and 2 with only a few rectangles on the edges of the survey areas, and in the centre of Survey 2, unsampled. On surveys 3 and 4 large areas in the centre of the survey and extending to the northern boundary were not sampled (see Figures 3.1.1 q and r). These areas, unsampled on surveys 3 and 4, were sampled at the equivalent time in 1985. During the 1985 surveys, some additional sampling was done in areas which had also been sampled in 1984. This was to provide an overlap in the coverage for comparison between the two years.

The Working Group decided that some extrapolation would have to be made for both unsampled rectangles and for large unsampled areas in 1984.

4.2 Extrapolation for unsampled sub-rectangles

To obtain values for rectangles on the edges of the survey area and for other small areas of unsampled sub-rectangles, a method similar to that used in the Western mackerel egg surveys was used (Lockwood et al. 1981). The convention followed was to use the logarithmic mean of values in adjacent sub-rectangles to provide an estimate for the unsampled sub-rectangle. Before an extrapolation could be made, a minimum of two adjacent observed values were required. Sub-rectangles immediately adjacent or diagonally adjacent to an unsampled sub-rectangle were accepted. No extrapolated values were used to calculate values for other unsampled sub-rectangles.

The contribution of the extrapolated values for unsampled sub-rectangles to the total production for each stage in each area is shown in Tables 4.4.1 to 4.4.3. Their contribution was generally less

than 11% for all stages with the exception of stage IV eggs on survey 3 where they contributed 25% to the total.

4.3 Extrapolation for unsampled areas

The intention of the Working Group was to use the data collected in 1985 to provide an estimate for the large unsampled areas in 1984. Examination of the 1985 data showed that a ratio could be calculated from the 84/85 overlap areas. However the abundance in the previously unsampled areas on both surveys was close to zero. After comparing the distributions in 1984 and 1985 it was decided that an increment close to zero for the unsampled areas on both surveys was unrealistically low. The main source of differences between the two years was difficult to identify. However the severe winter of 1985 may have been a contributing factor, in producing both temporal and spatial changes in spawning. As a result, use of the 1985 data in extrapolation for areas unsampled in 1984 was rejected. Instead a method was devised to use the 1984 data alone to estimate values of production for areas unsampled on surveys 3 and 4. Using the unsampled area on survey 3 as an example, the method used was as follows (Fig. 4.3.1).

- i. An appropriate survey was selected where the unsampled area on survey 3 was sampled (in this example, survey 2)
- ii. Areas which were sampled on surveys 2 and 3, adjacent to and covering the same range of latitude as the unsampled area on survey 3 were selected.
- iii. The mean abundance for each egg stage in the comparable areas on surveys 2 and 3 was calculated and the ratio between them was used as a raising factor.
- iv. The mean abundance as number $m^{-2}d^{-1}$ on survey 2 in the area unsampled on survey 3 was calculated. This was raised by the raising factor in iii. above.

- v. The adjusted mean production by the area unsampled in survey 3 was raised to give total production for this area.

The comparable areas used to extrapolate for the unsampled area on survey 4 are shown in Figure 4.3.2.

In this way estimates of production were obtained for each stage in the unsampled areas on Survey 3 and Survey 4. In both surveys there was an unsampled area at the northern edge of the grid for which no comparable data were available on other surveys. No attempt was made to estimate production in these areas. However abundance of eggs in the surrounding sampled rectangles suggests that the contribution of this unsampled area to production was negligible.

The validity of this method of extrapolation was checked using comparable areas on surveys 2 and 3, sampled in both periods (Figure 4.3.3). The reference areas A on surveys 2 and 3 were used to produce a raising factor by which area B on survey 2 could be used to provide an estimate of production in the same area on survey 3 (Fig. 4.3.3). The estimated values for each stage, as mean numbers $m^{-2}d^{-1}$ for survey 3, area B and the observed values in that area are given in Table 4.3.1. The values in area A used to calculate the raising factor and the resultant potential errors are also shown.

4.4 Production and mortality

The production values for each stage for observed sub-rectangles, extrapolated sub-rectangles and extrapolated areas, were summed for each stage to give total production on each survey. These calculations were made for the whole survey area (Table 4.4.1), for the North Sea only (Table 4.4.2) and for the eastern Channel (Table 4.4.3).

The survey periods in each area were used to calculate the beginning and end of the seasonal production curves and the survey mid points (Table 4.4.4). Total production values for each stage from Tables 4.4.1

to 4.4.3 were plotted against mid survey time, to produce seasonal production curves for each stage in each area. (Figure 4.4.1 a to c). The area under each curve, which represents the total seasonal production of each stage, was calculated by trapezoidal integration. These seasonal production values together with the instantaneous daily mortality rate (Z) between stages are shown in Table 4.4.5. The mortality rate Z is

$$Z = \frac{N_0 - N_t}{t}$$

calculated from the equation $N_t = N_0 e^{-Zt}$ where N_0 are the numbers in one stage, N_t the numbers surviving to a subsequent stage and t is the time

in days between those stages. An estimate of the number of fertilised eggs for each area is also given in Table 4.4.5. This value is calculated from the stage I-II mortality projected back to zero time.

The plot of \ln of production of each stage, for the North Sea and Eastern Channel, against age is shown in Figure 4.4.2. The age is calculated from the mean seasonal age of each stage weighted by production. These plots both indicate a non-linear relationship, with mortality increasing with age. The intercept value of the linear regression will therefore be an overestimate of total fertilised egg production, and has not been used. A quadratic model does describe the age dependent mortality (Figure 4.4.3) and gives intercept values of $14.1 \cdot 10^{12}$ for the North Sea and $0.9 \cdot 10^{12}$ for the eastern Channel.

5. CONFIDENCE REGION FOR PRODUCTION ESTIMATES

5.1 Background

Confidence regions of the stage I-IV egg production estimates were made using a simple, robust, approach suggested by Pope and Woolner, 1984. This method avoids the use of logarithmic transformations by the assumption that the coefficient of variation (η) of the production of each sampled rectangle is constant. Given the value of (η) it is thus possible to calculate the total survey production and its variance by summing the rectangle production and by summing the squares of rectangle production. This latter value is then multiplied by the η^2 to give the variance:

$$\begin{aligned} \text{Production of sample rectangles/day} &= \frac{\sum \text{(rectangle production/day)}}{\text{all rectangles}} \\ \text{Variance (of sample (rectangles/day))} &= \frac{(\text{Production (of sample (rectangles/day))})^2}{\eta^2 \sum \text{(rectangle production/day)}^2} \end{aligned}$$

Further, let the multiplier of η^2 be described as SSQ. This should not be confused with the normal statistical usage. The problem is thus to estimate SSQ for a survey and to show that η is reasonably constant over rectangles and to estimate its value. For typical surveys no entirely satisfactory method exists for estimating η , but it is usually possible to obtain lower and upper limits using estimates obtained from replicated rectangles for the lower estimate and the residual variance of general linear models fitted to extensive models of log rectangle production for an upper limit.

This approach was used for the 1984 North Sea Sole Egg Survey estimates, with some modifications to allow for additional variation in the estimate of the production of sole eggs due to extrapolation for some areas which were not sampled in surveys 3 and 4.

The estimation of (η) is described in section 5.2 and the calculation of variance is described in section 5.3.

5.2 Estimation of coefficient of variation

Estimates of the within sub-rectangle variance were derived from sub-rectangles where more than one sample was taken during a survey. These were not intentional replicates in the true statistical sense i.e. they were not taken specifically from the same position, and also were not necessarily taken on the same day. Most of these sub-rectangles were coastal ones hence zero egg numbers were often interspersed amongst a series of higher values. All zero values were included in the calculations. In terms of Stage I values, the number of sub-rectangles with more than one sample for the four surveys were 8, 22, 24 and 17 respectively. In all surveys, 14 was the maximum sample size on which an individual estimate of the variance was based, the average sample size being 4. From the variances (and their corresponding arithmetic means) survey coefficients of variation were determined for each egg stage. These are given in Table 5.2.1, together with the overall value for each stage, which shows a constant coefficient of variation of 0.9 per sub-rectangle cell within each survey.

Using log transformation of the egg numbers, linear models were fitted over all the surveys for each stage using the computer package GLIM (Baker and Nelder, 1978). Unfortunately, due to the computer storage requirements of GLIM, the survey cell size had to be increased from sub-rectangle to rectangle. Together with time being a continuous variable, the large number of zero values (for Stage I over all four surveys these accounted for 35% of the values), and the fact that all rectangles were included, a higher estimate of η was consequently obtained. The log residual variance (σ^2) obtained from fitting a model of temperature and rectangle was 1.44 which gave the upper limit of η as

$$\eta = \sqrt{e^{\sigma^2} - 1} = 1.8$$

5.3 Calculation of the variance of the production estimates.

This was achieved by first calculating SSQ. Calculations of SSQ are shown in Table 5.3.1. For sampled rectangles this multiplier was simply obtained by summing the squares of rectangle production. This was then raised by a factor given by

$$\left(\frac{\text{Sum of sampled and extrapolated rectangle productions per day}}{\text{Sampled rectangle production per day}} \right)^2$$

Such extrapolation clearly will cause additional variation. The simplest way to estimate this was to consider that:

$$\begin{aligned} & (\text{CV of extrapolated production in survey 3})^2 \\ &= (\text{CV of equivalent region } n/m^2/d \text{ in survey 2})^2 \\ &+ (\text{CV of adjacent region } n/m^2/d \text{ in survey 2})^2 \\ &+ (\text{CV of adjacent region } n/m^2/d \text{ in survey 3})^2. \end{aligned}$$

Estimates of the latter three CV's were obtained as

$$\eta^2 \Sigma (n/m^2/d)^2 / (\Sigma n/m^2/d)^2$$

for each of the three regions where summation was over all sampled rectangles. The summation ratio for the three regions gave the result called "Factor" in Table 5.3.1. This Factor multiplied by (production in the extrapolated area)² gave a value of SSQ which, when added to the SSQ from the sampled and extrapolated rectangles, gave the total SSQ multiplier for η^2 from the survey. Having obtained the η^2 multiplier SSQs for each survey these were combined to give the total η for each egg stage.

The factors used to raise the production estimates for each survey in this integration were squared and used to raise the η^2 multipliers SSQ for each survey.

Table 5.3.2 sets out the calculations, the factors being given by $(T(\text{survey} + 1) - T(\text{survey}-1))/2$

where T is time of survey.

$$T(0) = 0$$

$$T(S) = 115.$$

Finally the overall multipliers were used to calculate the variance of production.

Estimates of production and its variance and coefficient of variation are shown in Tables 3.3.1 to 4. This suggests coefficients of variation of about 14% for the various egg stages. This value is of course dependent on the estimate of η made in Section 5.3.2 and is indicative of variance levels rather than a firm statistical estimate. Nevertheless it should give some idea of the weight that should be attached to this particular set of estimates. The values of variance and CV given in Table 5.3.3 are based on the lower estimate and CV would be doubled at the upper limit.

6. FECUNDITY

Fecundity studies were based on samples taken by the UK, Netherlands and Fed. Rep. of Germany. The areas in which the samples were collected is shown in Fig. 6.1.

6.1 Methods

6.1.1 UK data. A total of sixty three fish were collected by commercial trawler in April 1983, April and May 1984 and in May 1985. The method used to process the sole gonads has been described by Witthames and Greer Walker (in press). The complete ovary was removed and preserved in Gilson's fixative for 5 months or more to separate the eggs from the associated gonadial tissue. The separated eggs were counted automatically using a HIAC particle counter after excluding eggs less than 200 μm and greater than 1000 μm . In 1983 all stage IV gonads were treated in this way. In 1984 and 85 an improved method of estimating fecundity was used (Greer Walker, Witthames and Davies, in press). Histological sections of the ovary were removed before separating the eggs in Gilson's fluid. Using the histological sections a number of apparently stage IV ovaries were found to contain post-ovulatory follicles which indicated that the fish had in fact spawned and these sample were excluded from further analysis.

The accuracy of the HIAC counter was examined by making replicate counts on 7 samples in 1984 and 13 samples in 1985. The mean difference between the samples was compared with an expected difference of zero using a t-test (Table 6.1.1). No significant differences were found for either year.

A further check on the HIAC counts was carried out by comparing replicate samples counted volumetrically using a Stempel pipette with samples counted through the HIAC. The results for the 4 samples treated

in this way are given in Table 6.1.2. The replicate HIAC counts for each sample had a lower variability than the counts done manually and the mean particle counts by HIAC varied from 10% less than to 14% more than the manual estimate. Analysis of the mean counts showed that the differences between the two methods were not significant at the 5% level and indicated that the HIAC counts would be used as an unbiased estimate of the fecundity.

6.1.2 Netherlands data. A total of 34 fish were selected for analysis from March 1980, March and April 1983 and in April 1984. Samples from other months were not processed. The ovaries were removed and preserved in alcohol before transferring to Gilson's fluid. Subsequent analysis was the same as the method used for the 1983 UK samples. Repeat counts of 10 samples gave comparable results confirming the reliability of the original analyses (Table 6.1.1).

The oocyte count for sample number 63 was abnormally low and this fish was excluded from further analysis.

6.1.3 German data. A total of 162 stage IV soles caught in the German Bight by a commercial trawler between end of March and end of April 1984 were analysed. Those gonads containing hyaline eggs were not considered. As described by Rosenboom (1985) the gonad membranes were dissolved in Gilson's fluid and the eggs were graded by a set of sieves into 9 fractions. Oocytes smaller than 0.2 mm were not considered to be spawned in the same year. The total number of eggs per female was found by means of the dry weight of the eggs in each fraction. The relationship between dry weight and egg number for each fraction had been found by manual counts on 3 fish - the variability of these calibrations was low.

6.1.4 Errors in estimation of fecundity

A number of factors could lead to errors in the estimation of fecundity. In particular there are doubts about the exclusion of small eggs

from the estimates. Venema (1964) and Deniel (1981) found no eggs over 0.25 mm in the ovaries of spent females which suggests that these smaller eggs are not spawned in the present year but form the basis for spawning in the following year. However recent studies (Greer Walker, pers. comm.) suggest that a proportion of the eggs as small as 0.14 will undergo vitellogenesis and may be spawned.

In the fecundity estimates carried out for the sole egg survey all eggs above 0.2 mm were included. These estimates will therefore include some eggs which will not develop (up to 10% of oocytes in the UK and Netherlands samples were between 0.2 and 0.25 mm). The estimate will also exclude a proportion of eggs below 0.2 mm which may have developed. There is not sufficient evidence to suggest whether these errors will significantly bias the fecundity estimate.

Another potential source of error comes from the eggs which are counted but subsequently do not develop into viable eggs. The histological techniques developed by Greer Walker et al. (in press) indicate that a variable proportion of the counted eggs may atrophy and not be spawned. The 1984 and 1985 samples collected by the UK showed that atrophied eggs may make up to 16% of the total in some fish. If no correction is made this could lead to a systematic overestimate of fecundity.

6.2 Results

The relationships between egg number and total fish weight (including guts and gonads) for each of the three countries are shown in Fig 6.2.1. The Netherlands total weights were calculated from gutted weight using a raising factor of 1.11. The increase in egg numbers with fish weight appears to follow an exponential curve of the form $y = a + x^b$. Log/log regressions of egg number (FEC) in thousands against total weight (TW) in g were calculated for each country.

UK : $\text{Ln FEC} = -2.925 + 1.360 \text{ Ln TW}$

Netherland: $\text{Ln FEC} = 0.602 + 0.768 \text{ Ln TW}$

Germany : $\text{Ln FEC} = -2.043 + 1.306 \text{ Ln TW}$

In order to see whether the data from the three countries could be combined to derive a single estimate of fecundity, a log/log fit of fecundity against weight was used to compare the slopes and intercepts of the three countries. Testing the reduction in the sums of squares using an F-test (Table 6.2.1) gave highly significant differences between the slopes ($F = 155$ for 2 and 240 d.f.) and a significant difference between the intercepts ($F = 4.25$ for 2 and 240 d.f.). Most of the unexplained variance appeared to come from the Netherlands data which had a very different slope and intercept compared to the German and UK data.

A comparison was therefore made between the German and UK data. Table 6.2.2 shows that there was little difference between the slopes of the two regressions but their intercepts were markedly different. This leads to a large difference in the absolute estimate of fecundity. From the German data, a fish of 600 g would have 42% more eggs than a sole of the same weight from the UK samples and 55% more than one from the Netherlands.

The apparently higher fecundity of fish from the German Bight suggests that there should be a higher relative gonad weight in these fish to account for the presence of the additional eggs. In order to test this possibility gonad weight was plotted against total weight for each country (Fig 6.2.2). There was little apparent difference between the countries and although comparisons of the slopes and intercepts of the combined data gave no significant differences between the slopes ($F = 1.27$ with 2 and 225 d.f.) there was a significant difference between the intercepts ($f = 6.45$ with 2 and 225 d.f.). If the UK and German data

are combined and tested against the model in which all the countries were separate, the reduction in the sum of squares was no longer significant ($F = 1.6$ with 1 and 227 d.f.) which suggests that the UK and German gonad weight data can be treated as similar.

The higher fecundity of fish in the German samples, despite having similar gonad weights to the UK fish, suggests that eggs may have been lost through spawning in some of the UK fish. It was hoped that this possibility might have been avoided by excluding all but stage IV ovaries from the analysis. However, it is difficult to be certain by visual examination whether a fish is just coming up to spawning or has recently spawned and is recovering. Histological examination of the UK samples in 1984 and 1985 showed that some fish which had been identified as stage IV had post-ovulatory follicles in their ovaries, indicating that these fish had previously spawned. Although these fish were excluded from the analysis it is possible that some of the ovaries from the Netherlands sole and the UK fish caught in 1983 may have spawned. The fish sampled by Germany were collected nearly one month earlier than the UK samples and would have been less mature. Some information on egg size distributions was available for the German samples in Figure 5 in Rosenboom (1985). This showed that no stage IV ovaries had eggs larger than 0.9 mm. By contrast, examination of the size frequency distributions of the UK and Netherlands samples indicated that there were two types of size distribution within the stage IV ovaries. Some fish had few eggs above 0.8 mm while between 30 and 48% of the ovaries had eggs greater than 0.9 mm in diameter.

The samples with eggs greater than 0.9 mm were excluded and the relationship between egg number and total weight re-examined. Although the trends in the curves for ovaries with small eggs moved closer to the

German line there was still a significant difference ($p < .01$) between the three countries Table 6.2.3.

Other factors which may have affected the fecundity estimates include area differences, year to year variation and the methods used to sort the samples. Area differences have been noted in plaice (Bagenall, 1986) although Rijnsdorp (1983) could find no significant differences. Differences between soles from two areas were examined by comparing the fecundity-weight relationship for soles collected by the Netherlands from rectangles 37F7 and 40F6 in the German Bight with Netherlands soles collected in other parts of the North Sea. The two regression lines are very similar, (but different from that of the German samples) suggesting that area differences can be excluded.

Year to year variation might be an important factor in fecundity variation. However, it seems unlikely to account for the large differences noted between the German estimate and those for the UK and Netherlands.

The final source of variation which was considered was the difference in the two sorting methods used. It was not possible to directly compare the two methods used for estimating egg numbers since the facilities for carrying out the analysis are no longer available at the Kiel institute. It was, therefore, recommended that samples are collected at the next opportunity and run through the HIAC particle counter followed by sieving to confirm that there are no consistent errors in the two methods.

In view of the inability to resolve the difference between the various fecundity estimates, it was decided that each of the estimates should be used separately to derive values for egg production.

6.3 Calculation of egg production

Egg production was calculated from the fecundity estimate using stock numbers and mean weights at age in the stock derived from a separate sex VPA for North Sea sole. Stock numbers were calculated for 1984 using the terminal mortalities and exploitation pattern given in the 1985 Flatfish WG report (Anon 1985b) except that a corrected age composition for 1984 and revised data for 1983 was used. For the egg production, the 1984 values for stock weight at age were taken. Maturity factors for female sole were calculated from Dutch market sampling data (ICES 1985b) and the average values for 1975-85 were used.

The data and results for the fecundity estimates derived from each of the three countries data are given in Table 6.3.1. The highest egg production was obtained from the German estimate which gave 20.6×10^{12} eggs. The UK and Netherlands estimates were similar at 12.1×10^{12} and 11.8×10^{12} respectively.

7. CONCLUSIONS AND RECOMMENDATIONS

7.1 General

Despite the difficulties which were encountered in obtaining some of the required samples, the 1984 ICES Sole Egg Survey has provided unique information on the spatial and temporal distribution of sole spawning, of the egg mortality rates and of production.

With the knowledge gained on the distribution of sole spawning it will be possible to design a more statistically efficient survey for estimating production in the future. The distribution was, and is likely to be, very patchy and the variance which was obtained for 1984 has been likened to a situation where all of the eggs occurred in only 10% of the samples.

Some problems have been encountered in ensuring that the identification and staging was carried out in an accurate and equivalent manner in each laboratory; future coordinated surveys will probably have to pay greater attention to this aspect.

The fecundity analysis has posed difficult problems both in the estimation technique and in the interpretation of the results. Work is already in hand to resolve this during 1986. Sole fecundity is difficult to measure principally because of the small oocyte size, the difficulty of identifying pre-spawning fish in a well-defined development stage and of allowing for atresia and the recruitment of young oocytes to the current season's spawning.

7.2 Conclusions

a. Centres of high sole egg ($>27 \text{ eggs.m}^{-2}$) production occurred in the following places:

- i) Baie de Somme (Eastern English Channel)
- ii) Belgian coast

- iii) Thames Estuary
- iv) Texel and Vlieland Ground
- v) Tade (Heligoland Bight)
- vi) Sylt Inner Ground (Heligoland Bight)

Lesser centres occurred off the Lincolnshire coast and in the Wash area, near the Norfolk banks and in the central Southern North Sea (Hinder to Schouwen Ground).

b. Production was strongly linked to season and peak production occurred later in the higher latitudes. Temperature (correlated with season and latitude) also explained a large proportion of the variation in production (positive effect) and production was greatest in the warmer, shallower water.

c. The egg mortality rate increased with age from about 15% per day between stages I and II to about 55% per day between stages III and IV. The possibility that this result is a biased result due to imperfect knowledge of the development rates cannot be completely ruled out, although the basic development rate data provided by Riley (pers. comm.) has been examined and has not found to be in error.

d. Total production of 'fertilised' sole eggs in the North Sea in 1984 was estimated to have been 15.5×10^{12} and that in the eastern Channel to have been 1.95×10^{12} eggs. The confidence limits on these estimates were judged to be $\pm 44\%$.

e. The Flatfish Working Group assessment of the stock biomass and age distribution of female sole in the North Sea for 1984 converted to a

potential egg production of either 12×10^{12} egg or 20.6×10^{12} depending upon which fecundity estimate was used (UK/Netherlands or German).

f. In the last analysis it has not proved possible to provide an independent estimate of sole stock biomass with which to confirm or deny the Virtual Population Analysis, principally because of the doubts about the fecundity of sole. All that can be said is that the female sole stock biomass in 1984 was either 18,000 or 31,120 tonnes \pm 44%, as opposed to the 23,400 tonnes given by the most recent VPA (1985 Working Group revised figure).

7.3 Recommendations

- a. That the experiments on development rate of sole eggs in relation to temperature originally performed by J. D. Riley, should be repeated to further ensure that the estimates of egg mortality rates have not been biased.
- b. That the fecundity analysis techniques of the UK and the Federal Republic of Germany should be compared by the collection of additional samples in the German Bight and Southern North Sea in 1986.
- c. That all of the plankton samples collected for the survey should be kept with a view to re-examination at a later date (staging, size of eggs etc.).
- d. That the results of the survey as expanded by recommendations a), b) and c), should be jointly published as a Cooperative Research Report.

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Table 2.2.1 Comparison of identification & staging; German samples

SHIP	DATE	STN	Egg Stage				Total Sole
			I	II	III	IV	
SOLEA	17.6.85	124	a) 268	8	119	0	395
			b) 231	106	43	3	383
SOLEA	18.6.85	143	a) 29	1	5	0	35
			b) 24	6	5	0	35
SOLEA	16.6.85	116	a) 17	2	4	0	23
			b) 16	3	3	0	22
SOLEA	16.6.85	117	a) 18	0	1	0	19
			b) 18	1	0	0	19
TOTAL			a) 332	11	129	0	472
			b) 289	116	51	3	459

a) as identified at Cuxhaven in 1985

b) as identified at Lowestoft during the meeting.

Table 2.2.2 Comparison of identification & staging; Dutch samples

SHIP	DATE	STN	Egg Stage				Total Sole	
			I	II	III	IV		
ISIS	22.5.85	24	a)	0	7	11	0	18
			b)	4	5	3	1	13
ISIS	21.5.85	15	a)	5	2	2	0	1
			b)	6	2	1	0	1
ISIS	21.5.85	11	a)	16	5	2	0	23
			b)	18	4	1	1	24
ISIS	21.5.85	12	a)	8	2	1	1	12
			b)	9	1	2	1	13
ISIS	28.5.85	26	a)	13	1	0	0	14
			b)	18	1	0	0	19
			a)	42	17	16	1	76
			b)	55	13	7	3	78

a) as identified at Ijmuiden in 1985

b) as identified at Lowestoft during the meeting.

ICES SOLE EGG SURVEY 1984

	(1, 2, 3 or 4)			
1. Survey number				
2. Ship's name				
3. Cruise identifier				
4. Order of occupation number				
5. Latitude				•
6. Longitude				•
7. ICES rectangle				
8. - sub-rectangle				
9. Date				
10. Time				
11. Mesh size				
12. True water depth				
13. Sampled depth				
14. Temperature - surface				•
15. - bottom				
16. Flowmeter revolutions				
17. Volume sampled				•
18. Count of Sole eggs - I				
19. - II				
20. - III				
21. - IV				
22. Count of sole larvea				

(Degrees, minutes;
east = 0, west = 1) .

(eg. 36 FO)

(see Figure 7)

(Day, month, year)

(GMT)

(µm)

(metres)

(metres)

(°C)

(°C, -99 if no value)

(number of revs)

(m³)

(total count)

"

"

"

"

(1, 2, 3 or 4)

REMARKS:	
NAME OF PERSON COMPLETING THIS FORM:	

Table 2.3.1 Data input form

Table 2.3.2 Validation checks on the basic data (data ranges for 1984)

FIELD	VALIDATION
5. Latitude	> 49.5 and < 56.5
6. Longitude	> -2.0 and < 9.0
7. Rectangle)
8. Sub-rectangle) Valid for Lat./Long.
9. Date	Day > 1 and < 30 or 31 Month > 3 and < 7 Year = 84
10. Time	> 0 and < 2359
13. Sampled depth	< water depth
14. Surface temperature	> 4.0
15. Bottom temperature	< surface temperature
16. Flowmeter revolutions	> 100 volume/rev < 0.1
17. Volume	> 5

	28	29	30	31	32	33	34	35	36	37	38	39	40	41	
E8															.888
															.888
															.888
															.888
															.888
E9															.538
															.538
															.888
															.948
															6.897
F0															26.564
															6.987
															59.827
															72.981
F1															91.765
															69.913
															185.492
															37.872
F2															33.887
															64.889
															314.818
															34.447
F3															13.531
															14.824
															22.738
															33.142
F4															23.871
															18.922
															28.467
															83.983
F5															17.381
															13.684
															6.881
															7.481
F6															5.888
															18.771
															.888
															18.935
F7															4.866
															7.887
															13.868
															4.397
F8															8.972
															8.897
															6.295
															.417

I.C.E.S SOLE EGGS SURVEY 2 NO/M.58 STAGE I EGGS

TOTAL 1273.818
FILE : A2NM1.CAL DATE PREPARED: 11/28/85

Table 2.3.3 Example spreadsheet of the sole egg survey results; ICES rectangle codes are given (north is to the right), a '+' indicates that the sample was for a quarter rectangle.

Table 3.3.1 ANOVA table for the model
based on Julian Day and
including a rectangle
effect (see EQ.1)

Effect	SS	df	MS
DAY + DAY ²	238	2	119
RECTANGLE	851	62	13.7
LATITUDE x DAY	101	1	101
ERROR	1597	1090	1.46
TOTAL	2787	1155	
R ²		43%	

Table 3.3.2 ANOVA table for the model
based on Julian day and
including all variables
separately (see EQ.2)

Effect	SS	df	MS
DAY + DAY ²	238	2	119
LATITUDE	172	1	172
LONGITUDE	109	1	109
LATITUDE x LONGITUDE	2	1	2
LATITUDE x DAY	249	1	249
DEPTH	135	1	135
ERROR	1882	1148	1.64
TOTAL	2787	1155	
R ²		33%	

Table 3.3.3 ANOVA table for the model
based on temperature and
including a rectangle
effect (see EQ.3)

Effect	SS	df	MS
TEMPERATURE + TEMPERATURE ²	712	2	356
RECTANGLE	474	62	7.6
LATITUDE X DAY	36	1	36
ERROR	1565	1090	1.44
TOTAL	2787	1155	
R ²		44%	

Table 3.3.4 ANOVA table for the model
based on temperature and
including all variables
separately (see EQ.4)

Effect	SS	df	MS
TEMPERATURE + TEMPERATURE ²	712	2	356
LATITUDE	73	1	63
LONGITUDE	94	1	94
LATITUDE x LONGITUDE	2	1	2
LATITUDE x DAY	87	1	87
DEPTH	58	1	58
ERROR	1771	1148	1.54
TOTAL	2787	1155	
R ²		36%	

Table 3.3.5 Regression parameters for eq. 2

Parameter	\bar{x}	S.E.
% GM	17.24	4.86
day	0.0491	.0196
day ²	- 0.001014	0.0000595
lat	- 1.115	.142
long	.0751	.2062
lat x long	- .0003706	.005667
lat x day	.006895	.0005408
depth	- .03006	.00332

Table 4.3.1 Potential error on the estimates of production in unsampled areas

Egg Stage	Survey	Mean numbers m^2d^{-1} (observed sub-rectangles)			
		Area A	Area B	Area B estimate on survey 3	% error
I	2	1.64	1.03		
	3	2.22	1.20	1.39	+ 14%
II	2	0.75	1.09		
	3	1.40	2.13	2.03	- 5%
III	2	0.14	0.33		
	3	0.22	0.71	0.52	- 27%
IV	2	0.028	0.063		
	3	0.055	0.157	0.124	- 21%

Table 4.4.1 Sole egg production in the North Sea and Eastern English Channel in 1984 (millions).

STAGE	I	II	III	IV
Observed rectangles				
SURVEY 1	18678.7	3111.7	360.2	155.7
2	172383.4	130661.6	28921.5	3626.8
3	231058.5	194151.5	44020.4	9227.7
4	95992.5	52714.9	30721.8	4420.7
TOTAL	518113.2	380639.8	104023.9	17431.0
Extrapolated rectangles				
SURVEY 1	354.4	19.3	2.3	.0
2	6111.5	4385.4	1441.5	369.0
3	18157.4	16932.4	5195.8	1782.0
4	11569.2	6965.2	3134.0	662.7
TOTAL	36192.5	28302.3	9773.6	2813.7
Extrapolated areas				
SURVEY 1	.0	.0	.0	.0
2	.0	.0	.0	.0
3	13384.6	13873.0	6079.7	1268.9
4	9596.5	23996.8	11211.1	3929.7
TOTAL	22981.1	37869.8	17290.8	5198.6
Total production				
SURVEY 1	19033.1	3131.1	362.5	155.7
2	178494.9	135047.0	30363.0	3995.8
3	262600.5	224956.9	55295.9	12278.6
4	117158.2	83676.9	45066.9	9013.1
TOTAL	577286.8	446812.0	131088.3	25443.2
Duration				
SURVEY 1	2.78	1.56	4.32	2.49
2	2.39	1.04	2.97	2.18
3	2.12	.90	2.51	1.99
4	1.58	.62	1.74	1.71
AVERAGE	2.12	.89	2.36	1.92

Table 4.4.2 Sole egg production in the North Sea
in 1984 (millions).

STAGE	I	II	III	IV
Observed rectangles				
SURVEY 1	9253.8	1396.2	104.8	.0
2	137713.4	99535.7	22785.1	3626.8
3	214579.7	177196.2	40154.1	8382.4
4	91442.6	47325.6	29373.6	3490.8
TOTAL	452989.4	325453.6	92417.6	15500.1
Extrapolated rectangles				
SURVEY 1	37.4	.0	.0	.0
2	5045.7	3768.9	1261.5	369.0
3	17701.1	16726.5	5053.8	1771.6
4	11421.3	6780.1	3060.3	627.1
TOTAL	34205.5	27275.5	9375.6	2767.7
Extrapolated areas				
SURVEY 1	.0	.0	.0	.0
2	.0	.0	.0	.0
3	13384.6	13873.0	6079.7	1268.9
4	9596.5	23996.8	11211.1	3929.7
TOTAL	22981.1	37869.8	17290.8	5198.6
Total production				
SURVEY 1	9291.2	1396.2	104.8	.0
2	142759.1	103304.6	24046.6	3995.8
3	245665.4	207795.7	51287.6	11422.9
4	112460.4	78102.5	43645.0	8047.6
TOTAL	510176.0	390598.9	119084.0	23466.3
Duration				
SURVEY 1	2.34	1.58	4.39	.00
2	2.37	1.02	2.95	2.18
3	2.12	.90	2.50	1.98
4	1.58	.61	1.74	1.69
AVERAGE	2.07	.88	2.31	1.91

Table 4.4.3 Sole egg production in the eastern Channel in 1984 (millions).

STAGE	I	II	III	IV
Observed rectangles				
SURVEY 1	9424.9	1715.6	255.4	155.7
2	34670.1	31125.9	6136.4	.0
3	16478.9	16955.4	3866.3	845.3
4	4549.9	5389.4	1348.2	929.8
TOTAL	65123.8	55186.2	11606.3	1930.9
Extrapolated rectangles				
SURVEY 1	317.0	19.3	2.3	.0
2	1065.8	616.5	180.0	.0
3	456.3	205.9	142.0	10.4
4	147.9	185.1	73.7	35.6
TOTAL	1987.0	1026.8	398.0	46.0
Extrapolated areas				
SURVEY 1	.0	.0	.0	.0
2	.0	.0	.0	.0
3	.0	.0	.0	.0
4	.0	.0	.0	.0
TOTAL	.0	.0	.0	.0
Total production				
SURVEY 1	9741.9	1734.9	257.7	155.7
2	35735.9	31742.4	6316.4	.0
3	16935.2	17161.3	4008.3	855.7
4	4697.8	5574.5	1421.9	965.4
TOTAL	67110.8	56213.0	12004.3	1976.9
Duration				
SURVEY 1	3.21	1.54	4.29	2.49
2	2.50	1.10	3.06	.00
3	2.16	.94	2.62	2.07
4	1.70	.65	1.81	1.77
AVERAGE	2.46	1.02	2.79	1.96

Table 4.4.4 Dates of the 1984 surveys, including the estimated dates on which spawning began and finished which were used for trapezoidal integration.

Survey	Dates	Midpoint Date	Day
<u>a) North Sea & English Channel; North Sea alone</u>			
Start		25 March	0
1	27 March-19 April	7 April	13
2	24 April-10 May	1 May	37
3	14 May-30 May	21 May	57
4	12 June-5 July	23 June	90
End		15 July	112
<u>b) Eastern English Channel</u>			
Start		15 March	0
1	27-29 March	28 March	13
2	24-26 April	25 April	41
3	21-25 May	23 May	69
4	17-19 June	18 June	95
End		30 June	104

Table 4.4.5 Estimates of production and daily mortality rates of sole eggs from the 1984 survey.

Stage	I	II	III	IV
NORTH SEA & CHANNEL				
prod E-12	14.4598	11.2914	3.3794	.6640
ln(prod)	2.6714	2.4240	1.2177	-.4094
age	1.0600	2.5600	4.1900	6.3300
T	1.5000	1.6300	2.1400	
-Z	-.1649	-.7401	-.7603	
exp(-Z)	.8480	.4771	.4675	
1-exp(-Z)	.1520	.5229	.5325	
No. of fertilised eggs (E-12)				17.2213
NORTH SEA ONLY				
prod E-12	12.9154	9.9529	3.0899	.6119
ln(prod)	2.5584	2.2979	1.1281	-.4911
age	1.0350	2.5100	4.1050	6.2100
T	1.4750	1.5950	2.1050	
-Z	-.1766	-.7334	-.7693	
exp(-Z)	.8381	.4803	.4634	
1-exp(-Z)	.1619	.5197	.5366	
No. of fertilised eggs (E-12)				15.5063
CHANNEL ONLY				
prod E-12	1.7468	1.4936	.3174	.0446
ln(prod)	.5578	.4012	-1.1476	-3.1091
age	1.2300	2.9700	4.8700	7.2500
T	1.7400	1.9000	2.3800	
-Z	-.0900	-.8152	-.8241	
exp(-Z)	.9139	.4426	.4386	
1-exp(-Z)	.0861	.5574	.5614	
No. of fertilised eggs (E-12)				1.9513

N.B. Estimates of fertilised eggs were obtained by correcting the no. of stage I eggs for the stage I to II mortality rate.

Table 5.2.1 Estimates of coefficient of variation
from replicate hauls

SURVEY	STAGE			
	I	II	III	IV
1	1.19	-	-	-
2	0.83	1.02	1.10	0.79
3	0.78	0.73	0.68	0.90
4	0.96	0.99	1.32	-
1-4	0.90	0.88	0.90	0.86

Table 5.3.1 Sums of squares calculations for the 1984 survey.

	STAGE I				STAGE II			
SURVEY	1	2	3	4	1	2	3	4
OBSERVED RECTS								
prod	16678.7	172383.4	231058.5	95992.5	3111.7	130661.6	194151.5	52714.9
ssq	33.2644	1502.4248	3625.9709	198.1385	.9848	1177.5094	2593.9893	74.6416
EXTRAPOLATED RECTS								
prod	354.4	6111.5	18157.4	11569.2	19.3	4385.4	16932.4	6965.2
ssq	34.5387	1610.8440	4218.2461	248.7766	.9971	1257.8775	3066.1748	95.6694
EXTRAPOLATED AREAS								
prod	.0	.0	13384.6	9596.5	.0	.0	13873.0	23996.8
factor	.0000	.0000	.4160	.1444	.0000	.0000	.4483	.2130
ssq	.0000	.0000	74.5254	13.2982	.0000	.0000	86.2799	122.6553
TOTAL								
prod	19033.1	178494.9	262600.5	117158.2	3131.0	135047.0	224956.9	83676.9
ssq	34.5387	1610.8440	4292.7714	262.0748	.9971	1257.8775	3152.4546	218.3247

	STAGE III				STAGE IV			
SURVEY	1	2	3	4	1	2	3	4
OBSERVED RECTS								
prod	360.2	28921.5	44020.4	30721.8	155.7	3626.8	9227.7	4420.7
ssq	.0335	38.8068	61.5959	51.4163	.0243	.8349	3.9865	1.2052
EXTRAPOLATED RECTS								
prod	2.3	1441.5	5195.8	3134.0	.0	369.0	1782.0	662.7
ssq	.0340	42.7716	76.9945	62.4415	.0243	1.0135	5.6749	1.5937
EXTRAPOLATED AREAS								
prod	.0	.0	6079.7	11211.1	.0	.0	1268.9	3929.7
factor	.0000	.0000	.5340	.2570	.0000	.0000	.5740	.4630
ssq	.0000	.0000	19.7381	32.3020	.0000	.0000	.9242	7.1499
TOTAL								
prod	362.5	30363.0	55295.9	45066.9	155.7	3995.8	12278.6	9013.1
ssq	.0340	42.7716	96.7326	94.7435	.0243	1.0135	6.5991	8.7436

N.B. Values of 'prod' and 'ssq' are E-06, with
ssq values calculated on 'prod' as E-06.

Table 5.3.2 Estimates of production for the 1984 survey
using trapezoidal integration, and their
coefficients of variation.

Production curve stage I

	T	Prod	RAISED	ssq	RAISED
0	0				
1	13	19033.1	352112.4	34.5	11820.9
2	37	178494.9	3926887.8	1610.8	779648.5
3	57	262600.5	6958913.3	4292.8	3014598.7
4	90	117158.2	3221850.5	262.1	198194.1
5	112				
total			14459763.9		4004262.1
standard deviation					.138
coefficient of variation					.125

Production curve stage II

0	0				
1	13	3131.1	57925.4	1.0	341.3
2	37	135047.0	2971034.0	1257.9	608812.7
3	57	224956.9	5961357.9	3152.5	2213811.2
4	90	83676.9	2301114.8	218.3	165108.1
5	112				
total			11291432.0		2988073.3
standard deviation					.153
coefficient of variation					.138

Production curve stage III

0	0				
1	13	362.5	6706.3	.0	11.6
2	37	30363.0	667986.0	42.8	20701.5
3	57	55295.9	1465341.4	96.7	67930.5
4	90	45066.9	1239339.8	94.7	71649.8
5	112				
total			3379373.4		160293.3
standard deviation					.118
coefficient of variation					.107

Production curve stage IV

0	0				
1	13	155.7	2880.5	.0	8.3
2	37	3995.8	87907.6	1.0	490.5
3	57	12278.6	325382.9	6.6	4634.2
4	90	9013.1	247860.3	8.7	6612.3
5	112				
total			664031.2		11745.4
standard deviation					.163
coefficient of variation					.147

N.B. Values of 'prod' and 'ssq' are E-06, with
ssq values calculated from 'prod' as E-06.

Table 5.3.3 Production, production variance and production CV for each egg state of the 1984 North Sea sole egg survey

Stage	Production x 10 ⁻¹²	Variance x 10 ⁻²⁴ *	Coef. of variance (%)*
I	14.5	4.00	12.5
II	11.3	2.99	13.8
III	3.4	0.160	10.7
IV	0.66	0.0117	14.7

*Calculated under the assumption $\eta = 0.9$

Table 6.1.1 Comparison of paired counts of eggs by HIAC

	UK		NETHERLANDS
	1984	1985	1983
No samples	7	13	10
Mean % difference	-4.46	-9.01	-6.48
S.d	22.85	16.96	10.34
t	0.517	1.987	1.980
	Not signif at p < 0.05	Not signif at p < 0.05	Not signif at p < 0.05

Table 6.1.2 Comparison of egg counts done volumetrically with Stempel pipette and by HIAC

Sample No	Stempel pipette		HIAC		% diff
	Mean count	s.d.	Mean count	s.d.	HIAC/Manual
27	42919	7693	44507	680	+ 3.7
32	44049	6035	49986	258	+ 13.5
40	45766	2959	49256	325	+ 7.6
46	39469	5205	35720	848	- 9.5
Replicate Mean	43501		44867		
SE of mean	2563.6		411.4		
95% conf. limits	± 8157		± 1309		

Table 6.2.1 Comparison of slopes and intercepts for each country using the model $\ln(\text{egg number}) = b + a \ln(\text{total weight})$

Source	SSQ	df	MS	F	level of signif
different slopes	25.51	2	12.76	155	0.01
different intercepts	0.70	2	0.35	4.25	0.05
Residual	19.78	240	0.08		

Table 6.2.2 Comparison of slopes and intercepts for UK and German data using the model $\ln(\text{egg number}) = b + a \ln(\text{total weight})$

Source	SSQ	df	MS	F	level of signif
different slopes	0.01	1	0.01	0.114	NS
residual	18.27	209	0.0874		
different intercepts	12.39	1	12.39	142	0.01
residual	18.28	210	.0871		

Table 6.2.3 Comparison of intercepts for each country after exclusion of ovaries with eggs > 0.9 mm, using model $\ln(\text{egg number}) = b + a \ln(\text{total weight})$

Source	SSQ	df	MS	F	level of signif
different intercepts	9.58	2	4.79	61.2	0.01
Residual	14.57	186	0.08		

	Slope	intercept
UK	1.328	-2.734
Netherlands	1.328	-2.821
Germany	1.328	-2.179

Table 6.3.1 Estimates of egg production for North Sea sole in 1984 from VPA cod fecundity data

Age	Stock w.a.a. (kg, whole weight)	Stock nos. ($\times 10^{-3}$)	Maturity factor	UK		Netherlands		Germany	
				Fecundity ($\times 10^{-3}$)	Egg production ($\times 10^{-6}$)	Fecundity ($\times 10^{-3}$)	Egg production ($\times 10^{-6}$)	Fecundity ($\times 10^{-3}$)	Egg production ($\times 10^{-6}$)
1	.025	45707	0	-	0	-	0	-	0
2	.133	41199	.06	41.5	102,586	78.1	193,059	77.0	190,339
3	.241	53114	.63	93.2	3,118,642	123.3	4,125,842	167.4	5,601,509
4	.356	23449	.95	158.4	3,528,606	166.3	3,704,590	278.6	6,206,247
5	.444	11926	1	213.9	2,550,971	197.1	2,350,615	371.7	4,432,894
6	.484	560	1	240.5	136,604	210.6	119,621	416.0	236,288
7	.584	977	1	310.5	303,359	243.2	237,606	531.7	519,471
8	.689	1786	1	388.7	694,218	276.2	493,293	659.9	1,178,581
9	.727	962	1	415.8	400,000	286.9	275,998	704.0	677,248
10	.816	312	1	489.3	152,662	314.5	98,124	823.0	256,776
11	.807	399	1	482.0	192,318	311.8	124,408	811.2	323,669
12	.908	358	1	574.3	205,599	344.3	123,259	959.9	343,644
13	.874	84	1	537.2	45,125	331.5	27,846	900.2	75,617
14	.953	67	1	604.3	40,488	354.3	23,738	1,007.9	67,529
15+	.909	570	1	566.7	323,019	341.7	194,769	947.6	540,127
					11,794,197				20,649,939
					$11.8 \cdot 10^{12}$				$20.6 \cdot 10^{12}$

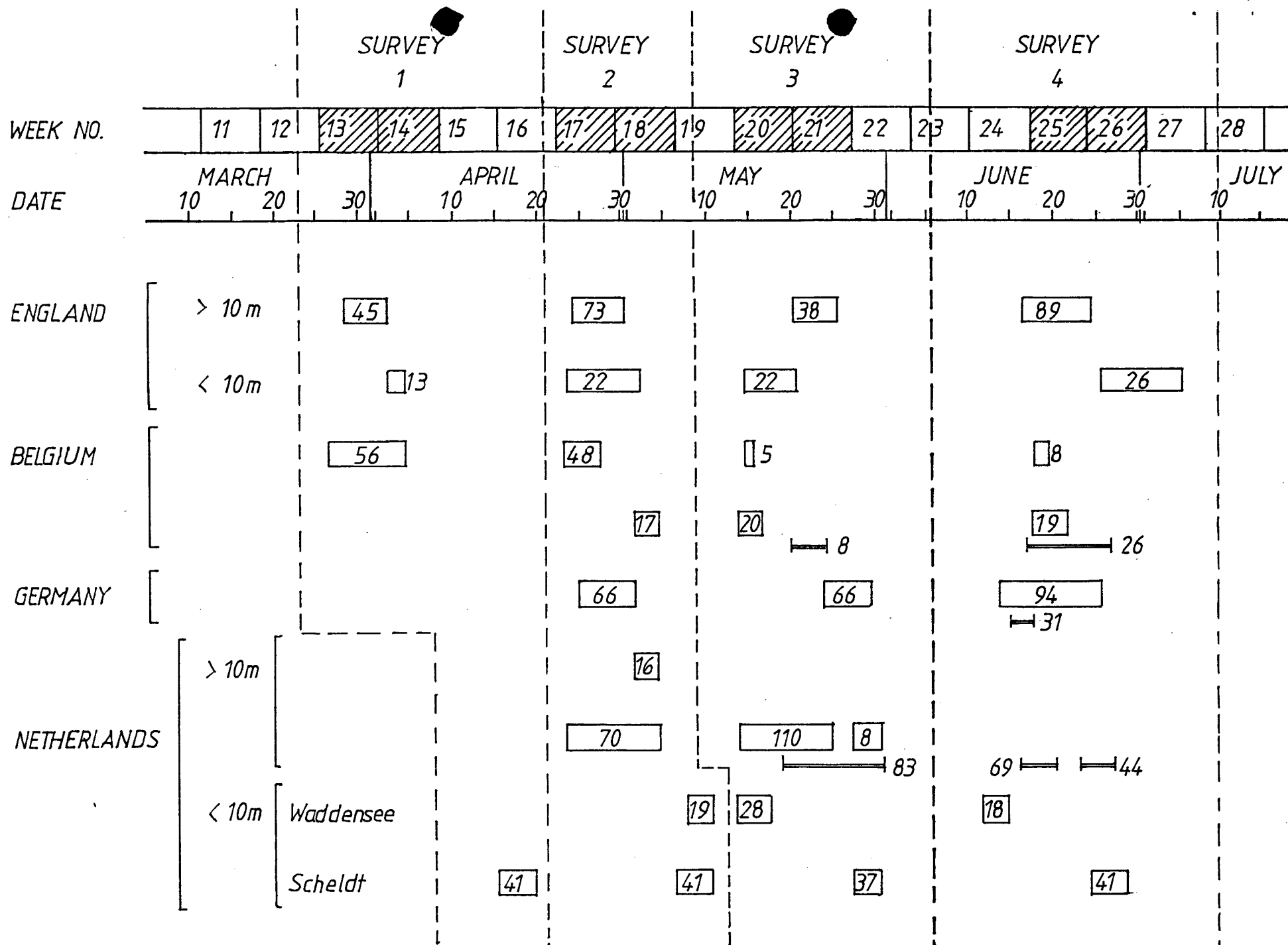


Figure 2.1.1 Number and origin of plankton samples for the 1984 and 1985 surveys (the latter shown as a double bar); the number of samples obtained on each cruise are shown, as is the allocation of each cruise to the four surveys.

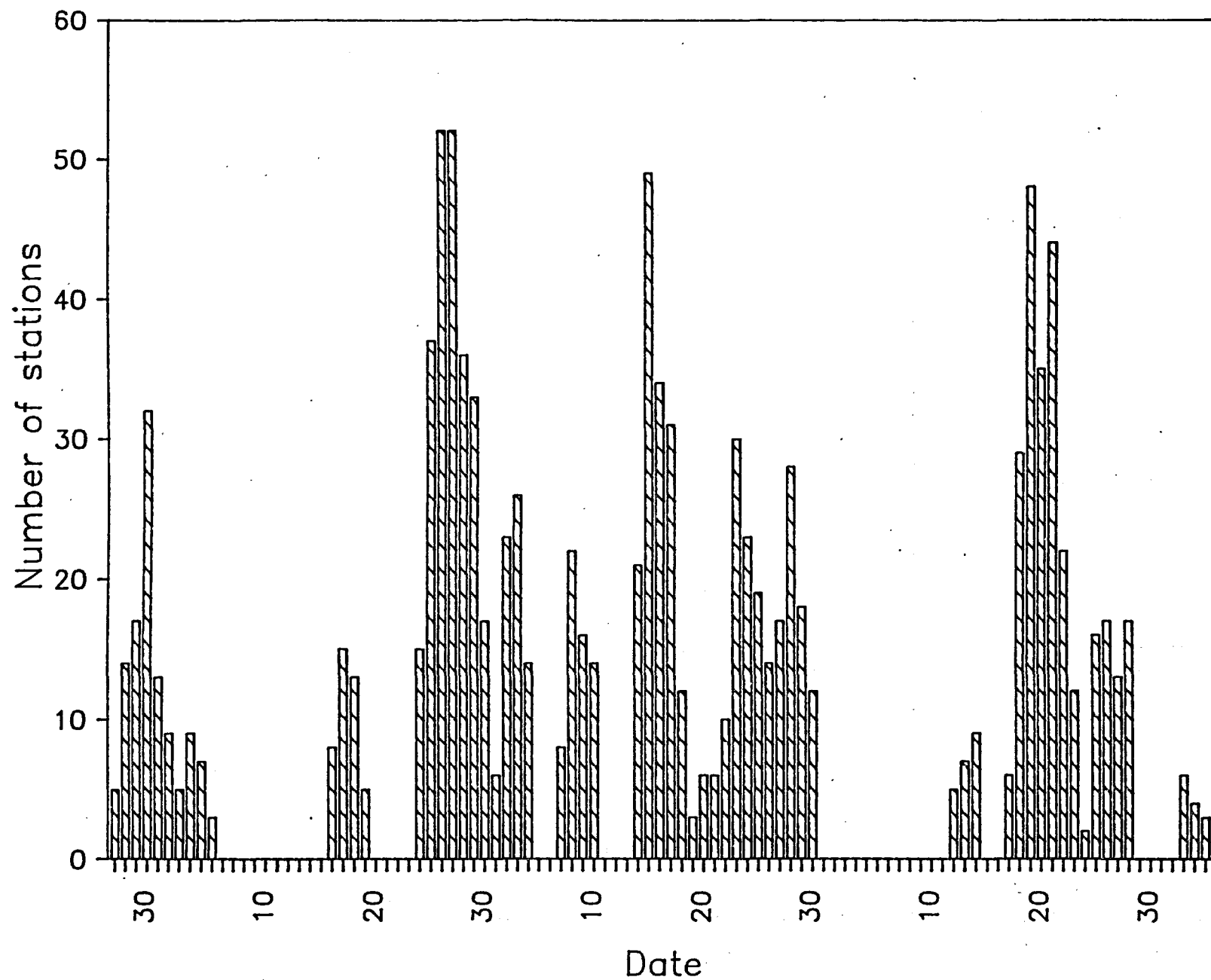


Figure 2.1.2 Frequency distribution of sampling in relation to date for 1984.

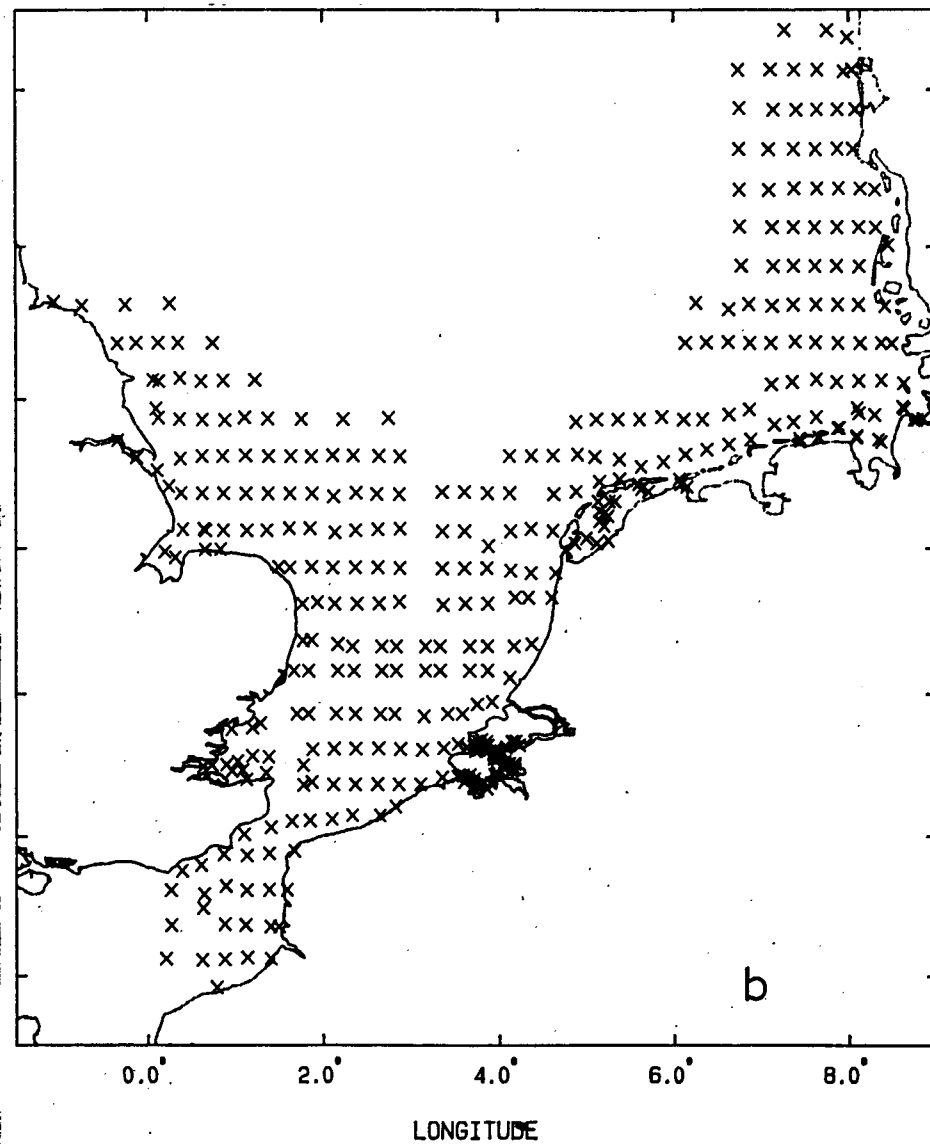
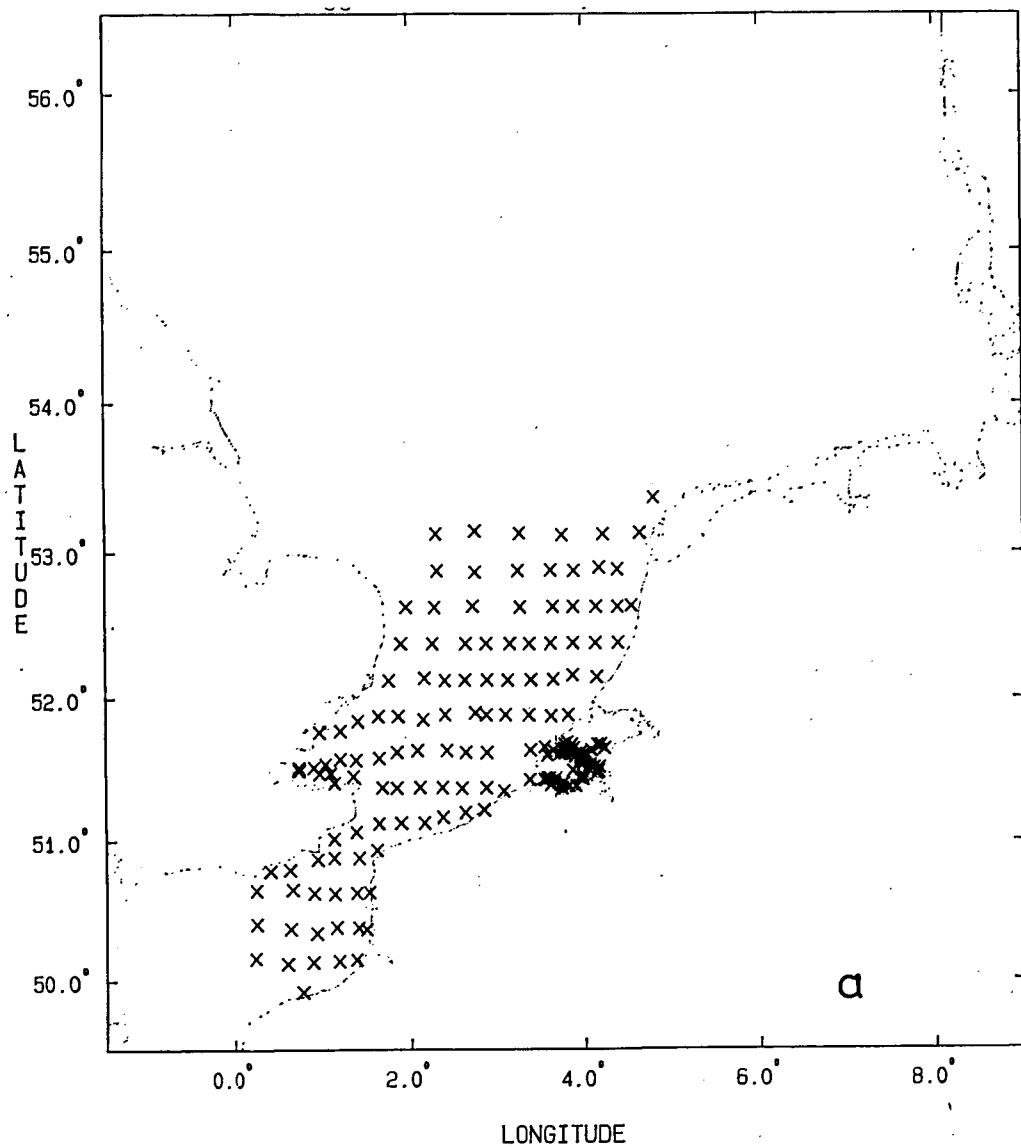
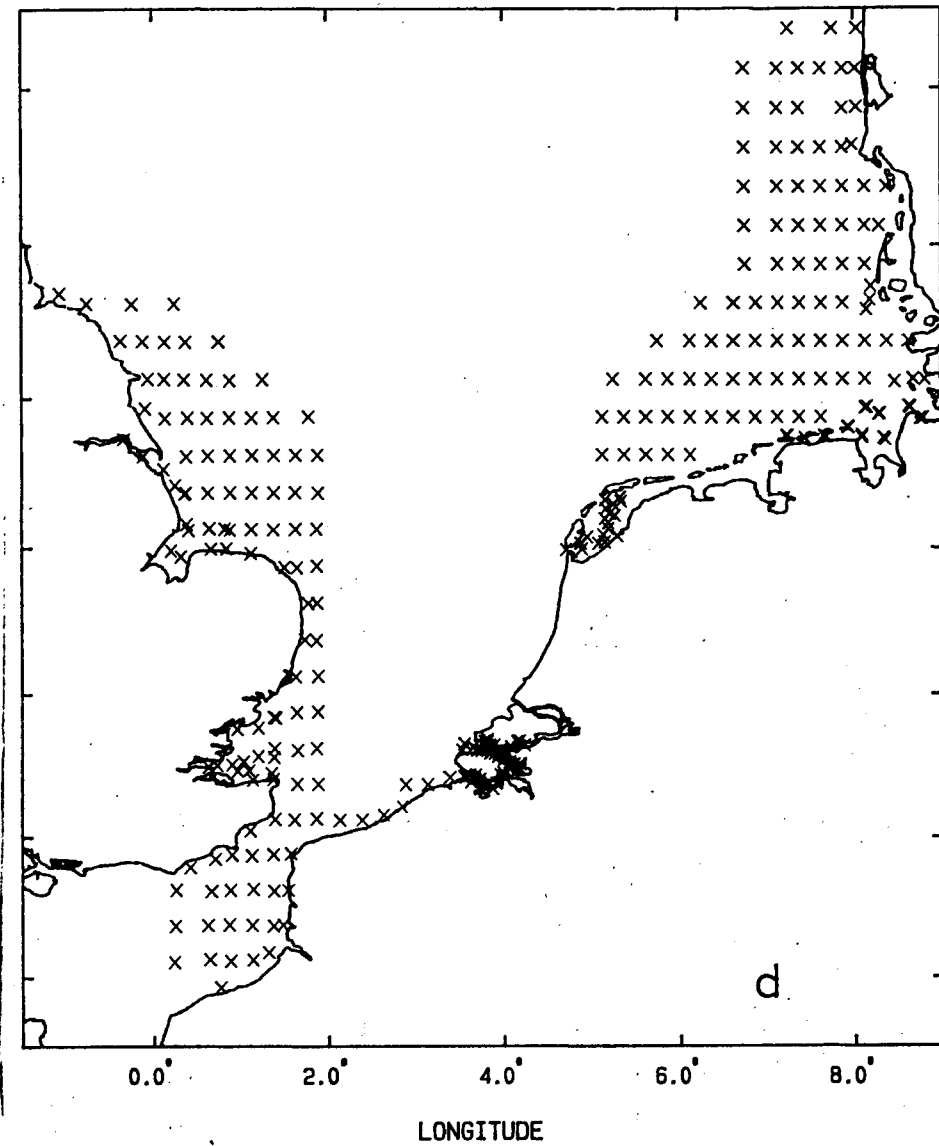
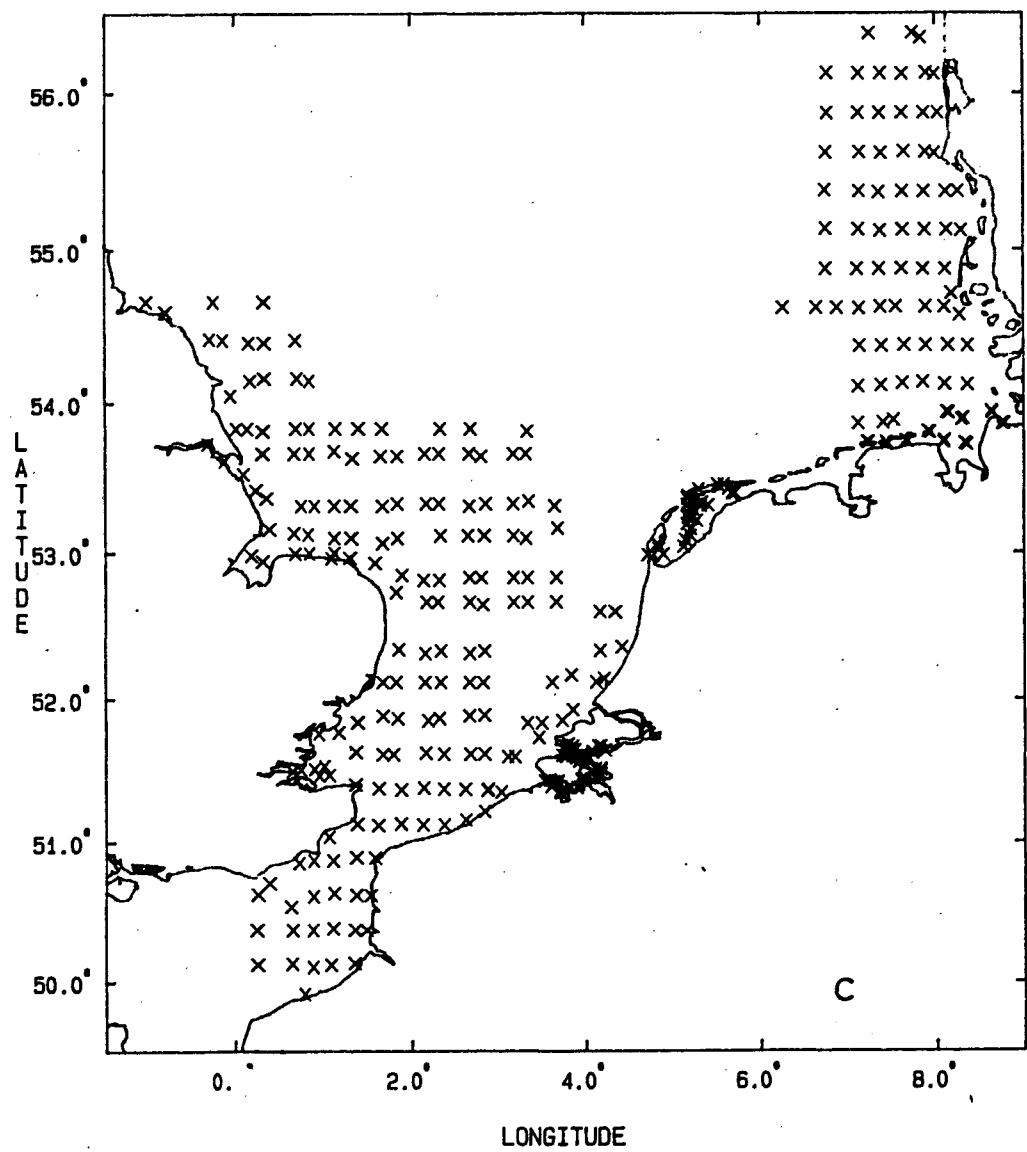


Figure 2.1.3a-d Positions of sampling in 1984: (a) survey 1,
(b) survey 2, (c) survey 3, (d) survey 4.



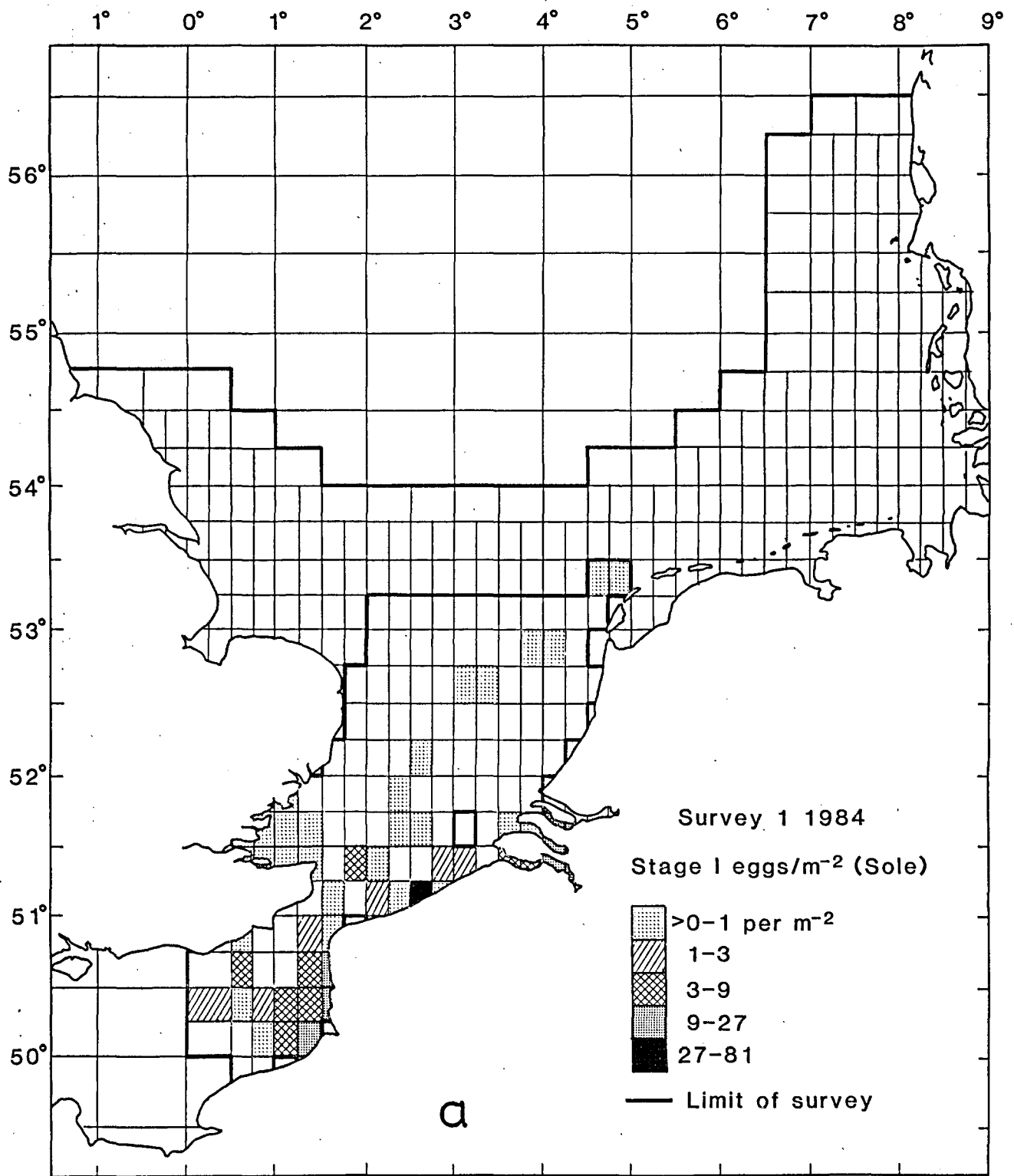
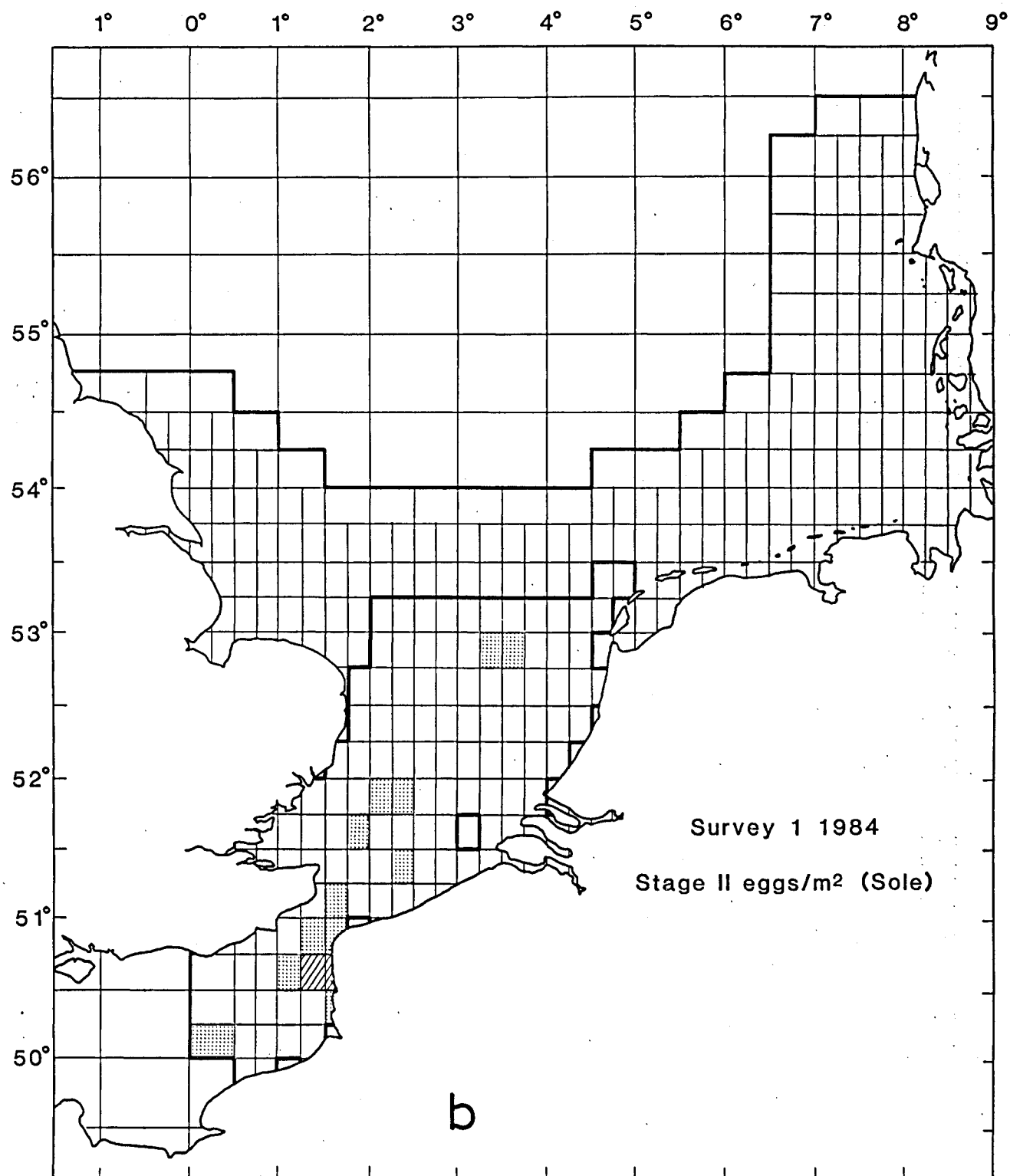
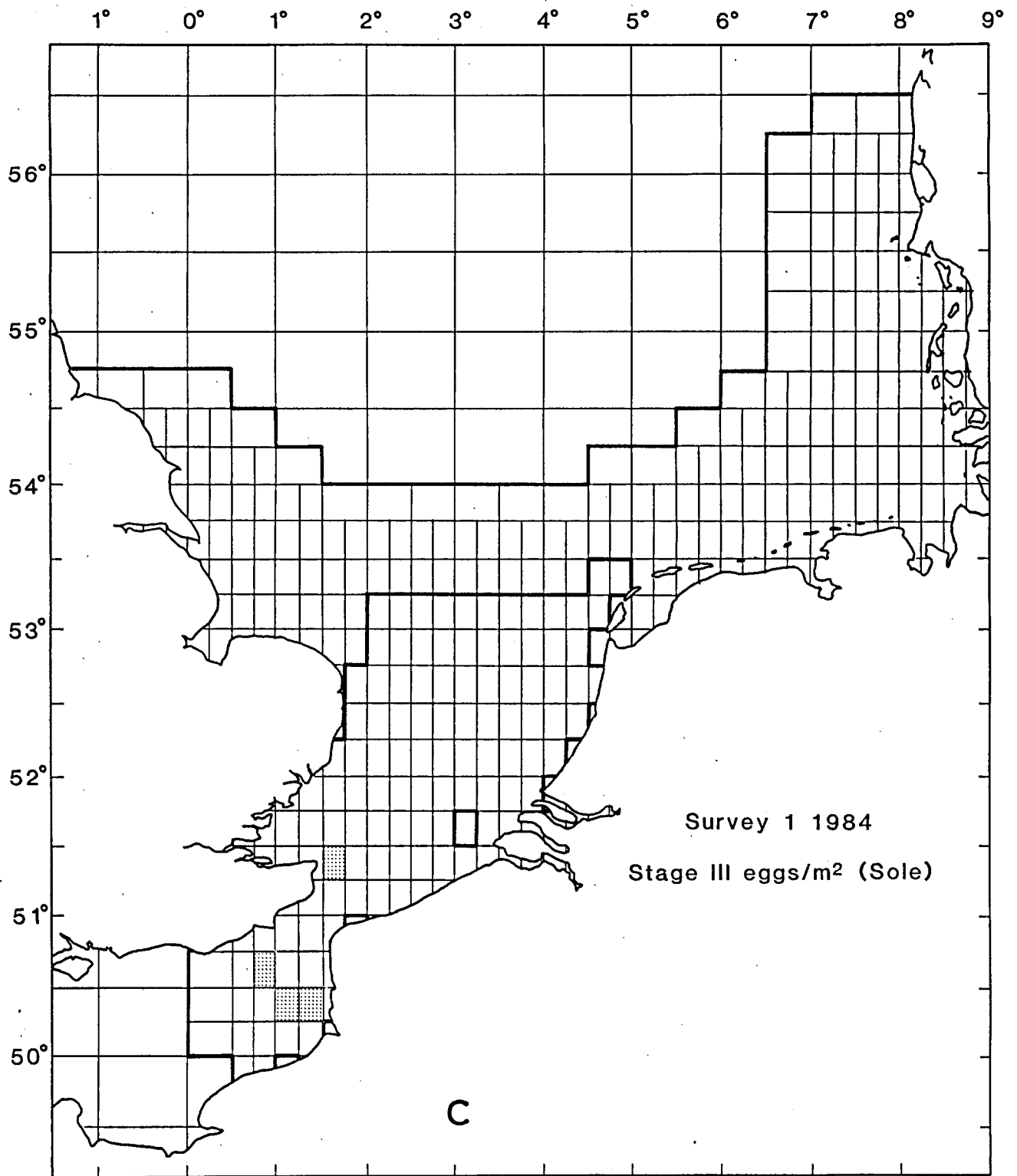
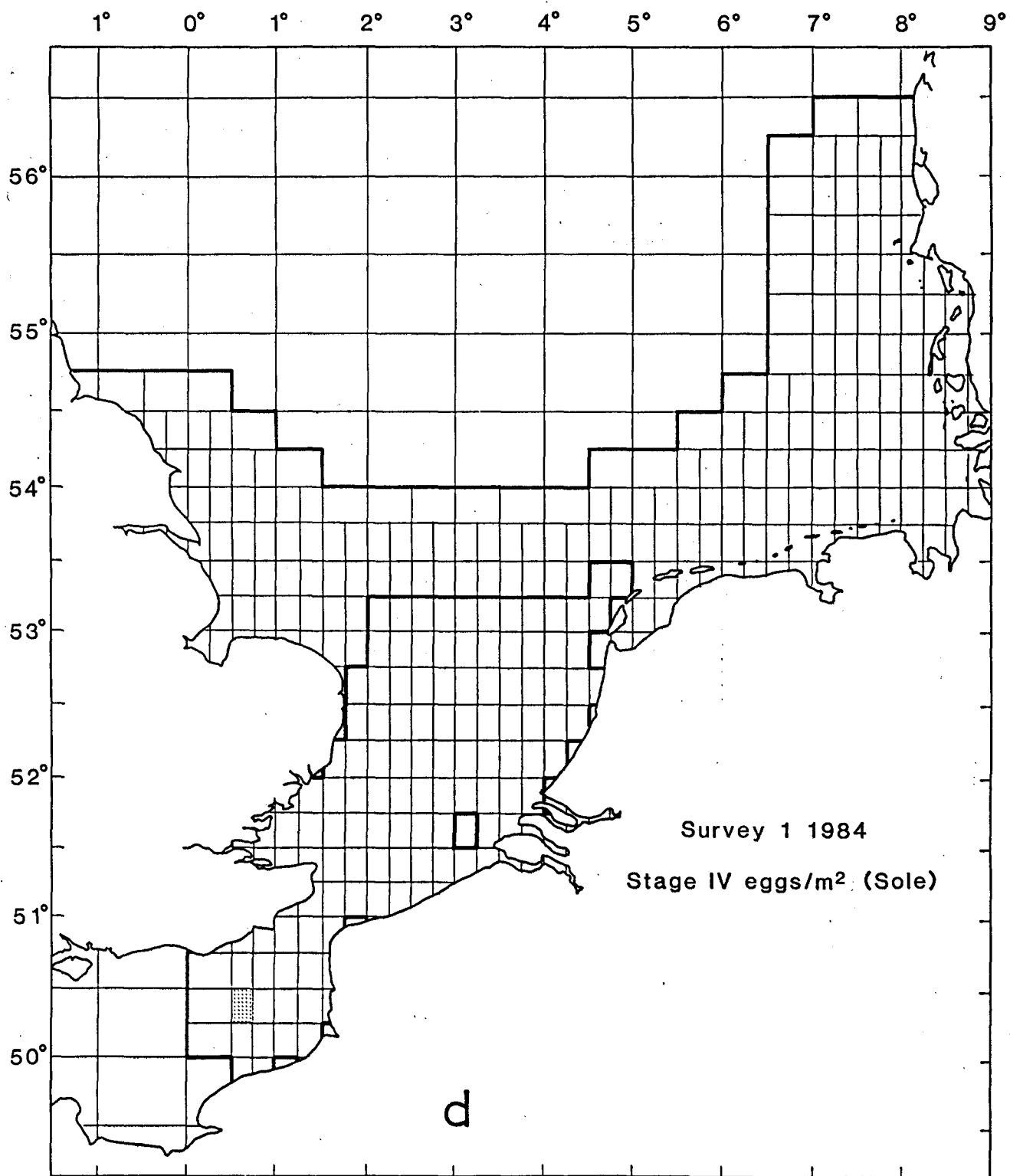
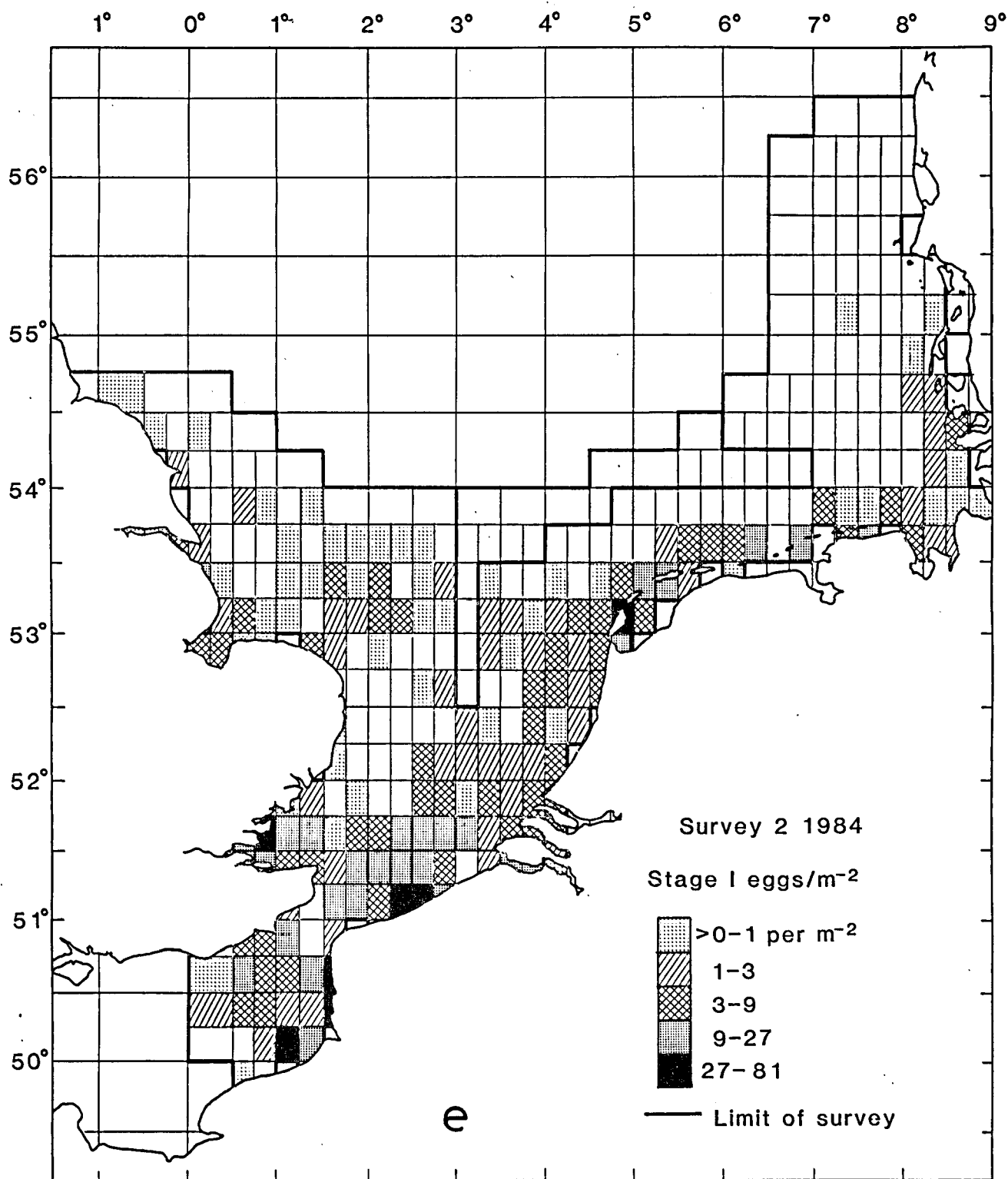


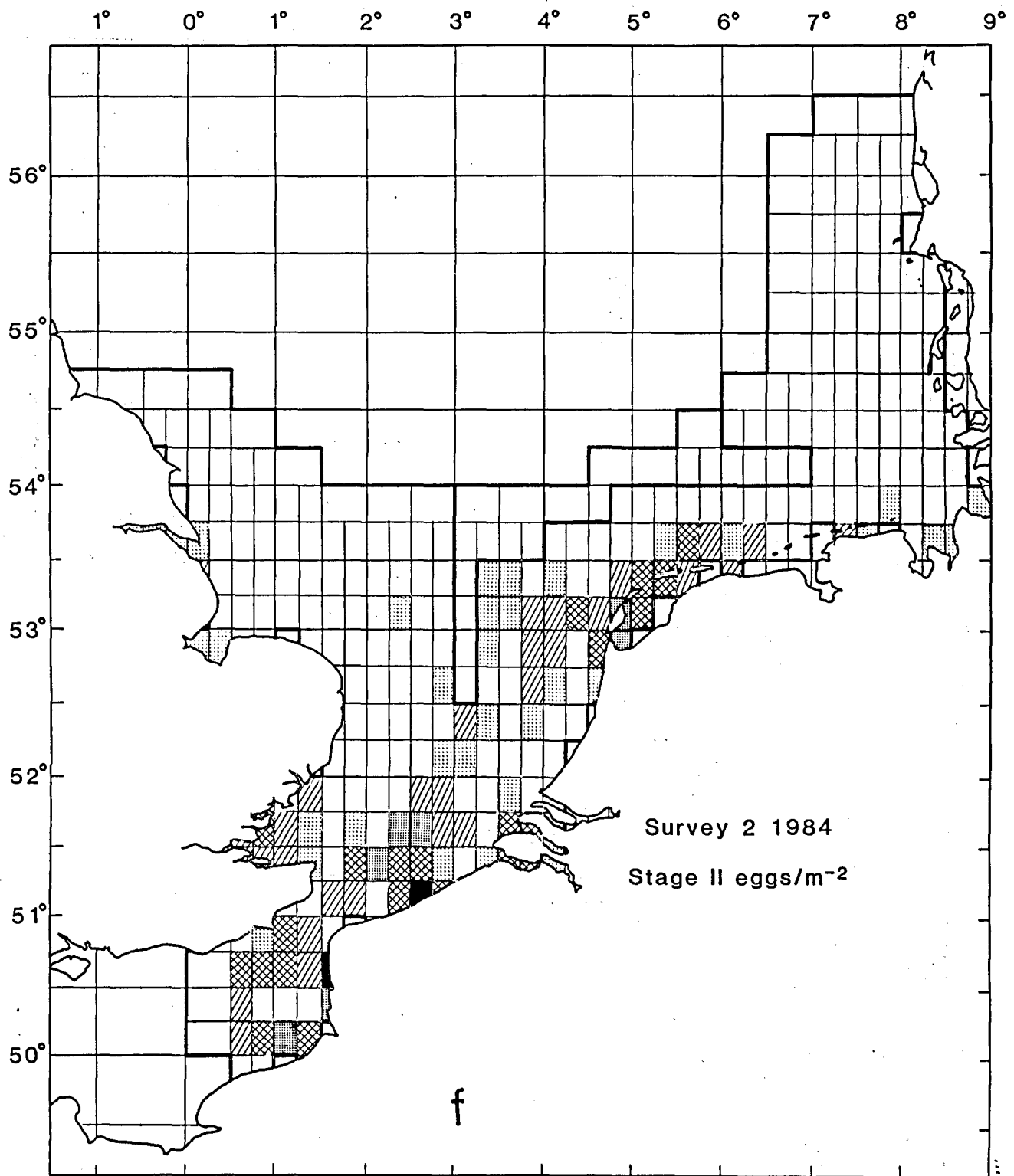
Figure 3.1.1a-r Abundance of sole eggs of each stage measured during the 1984 and 1985 surveys (no. m⁻²).

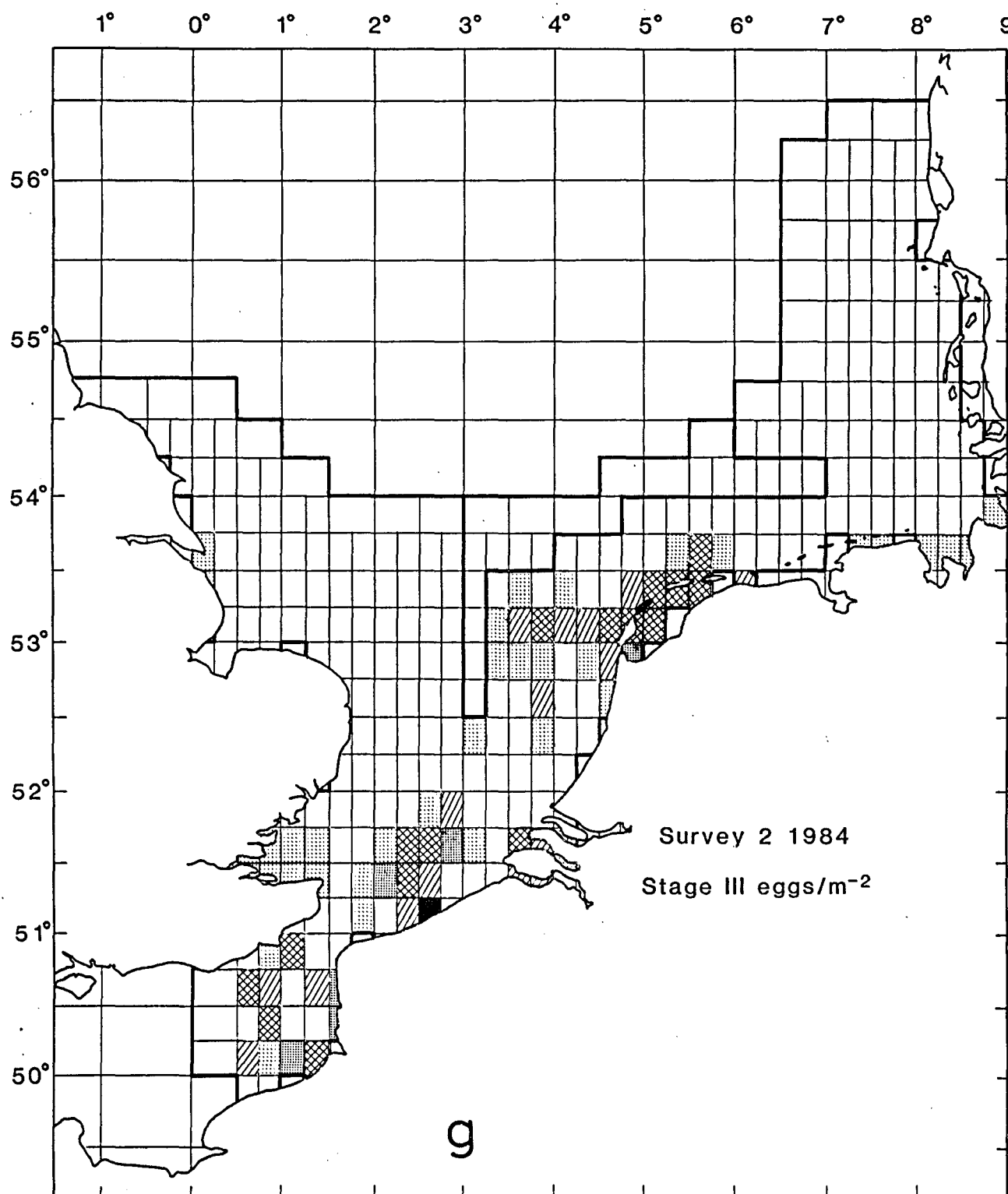


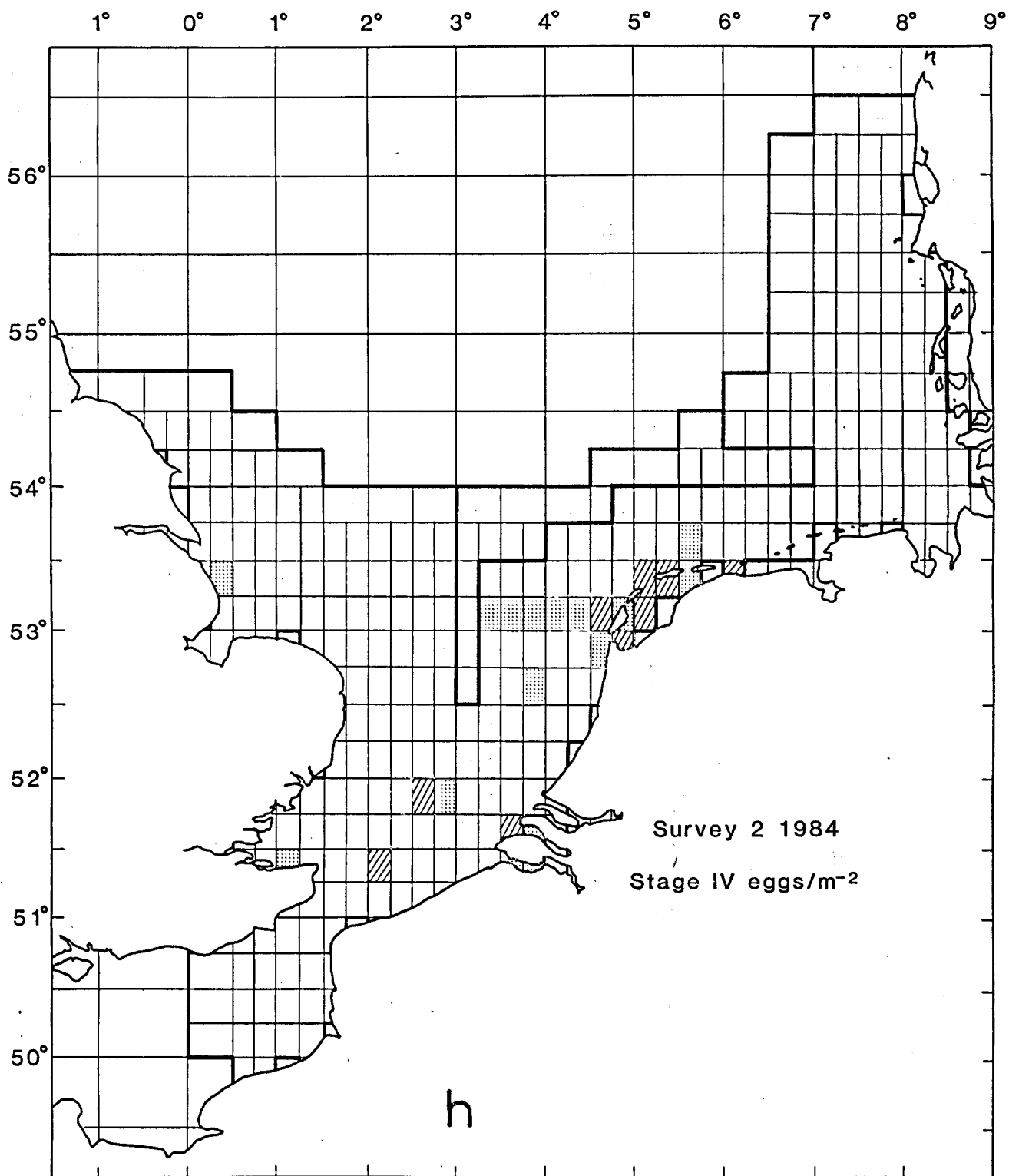


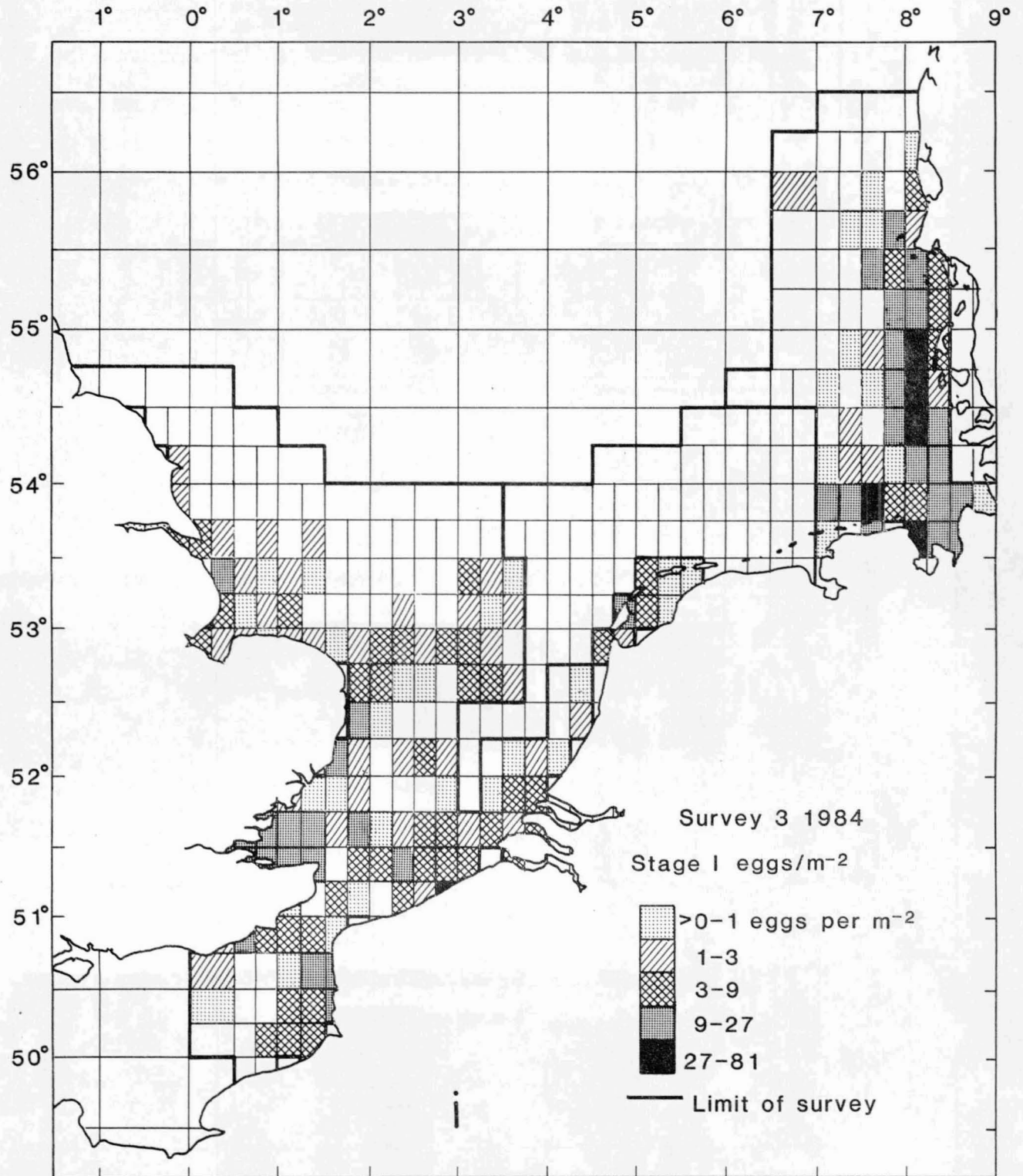


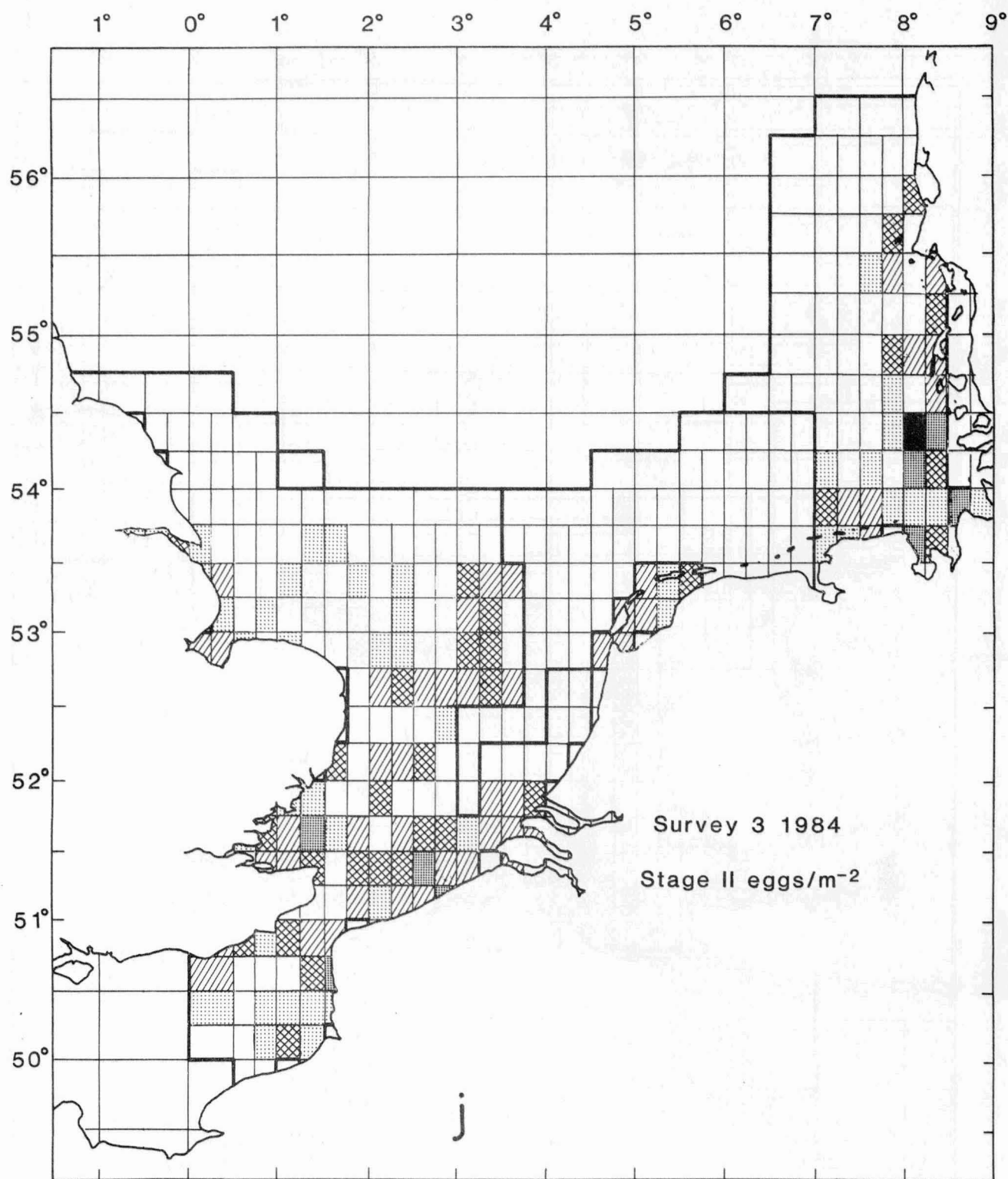


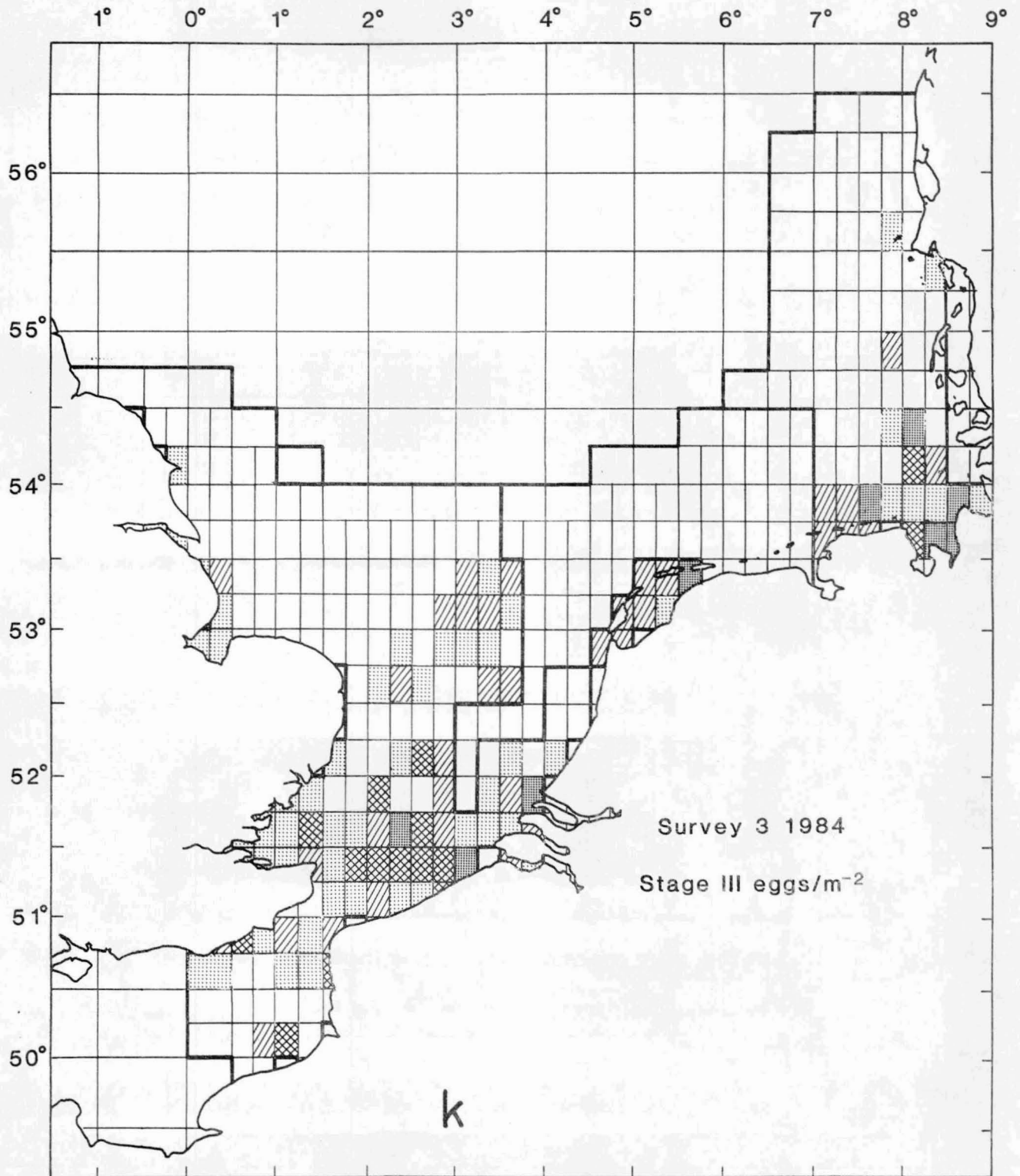




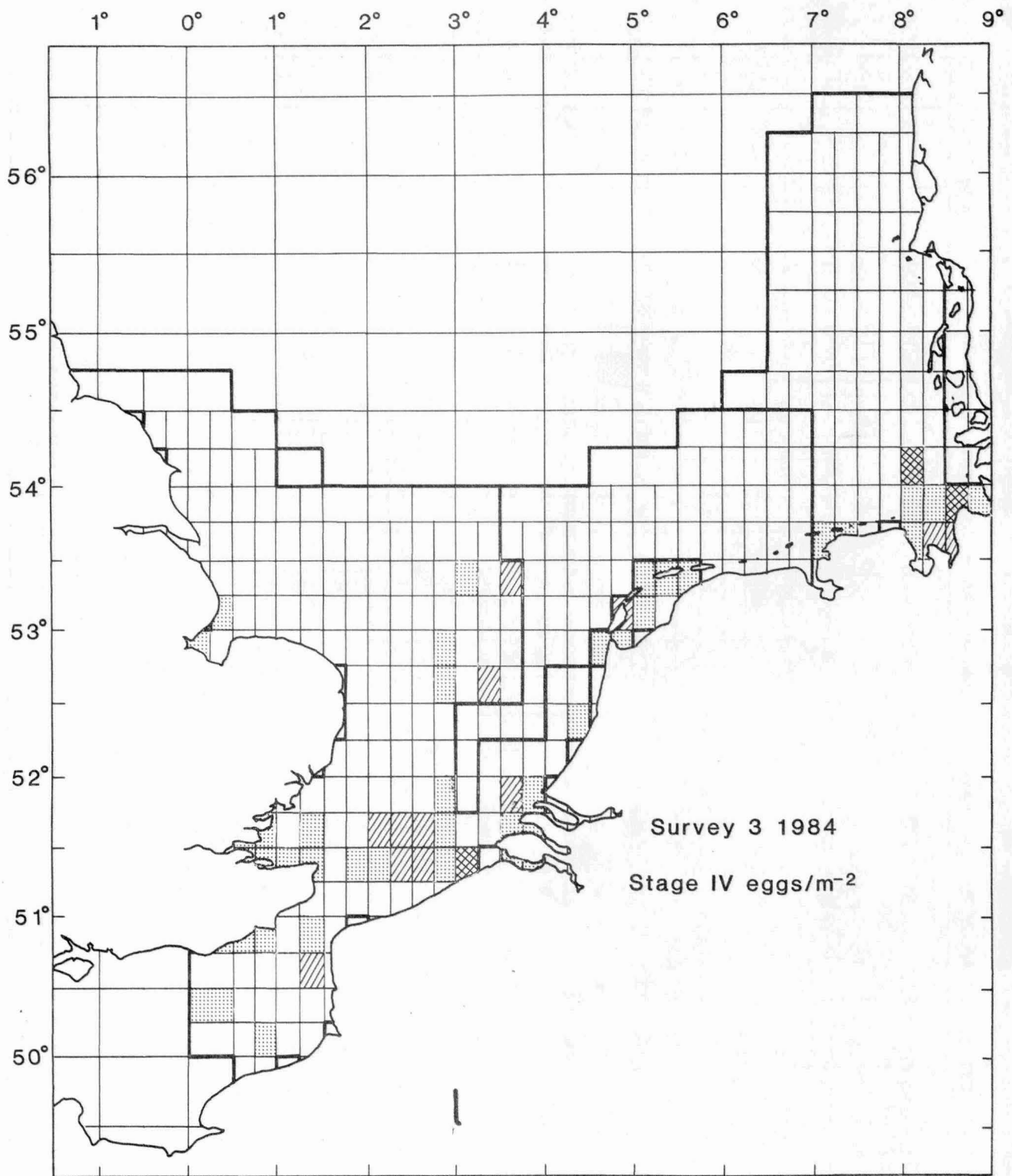


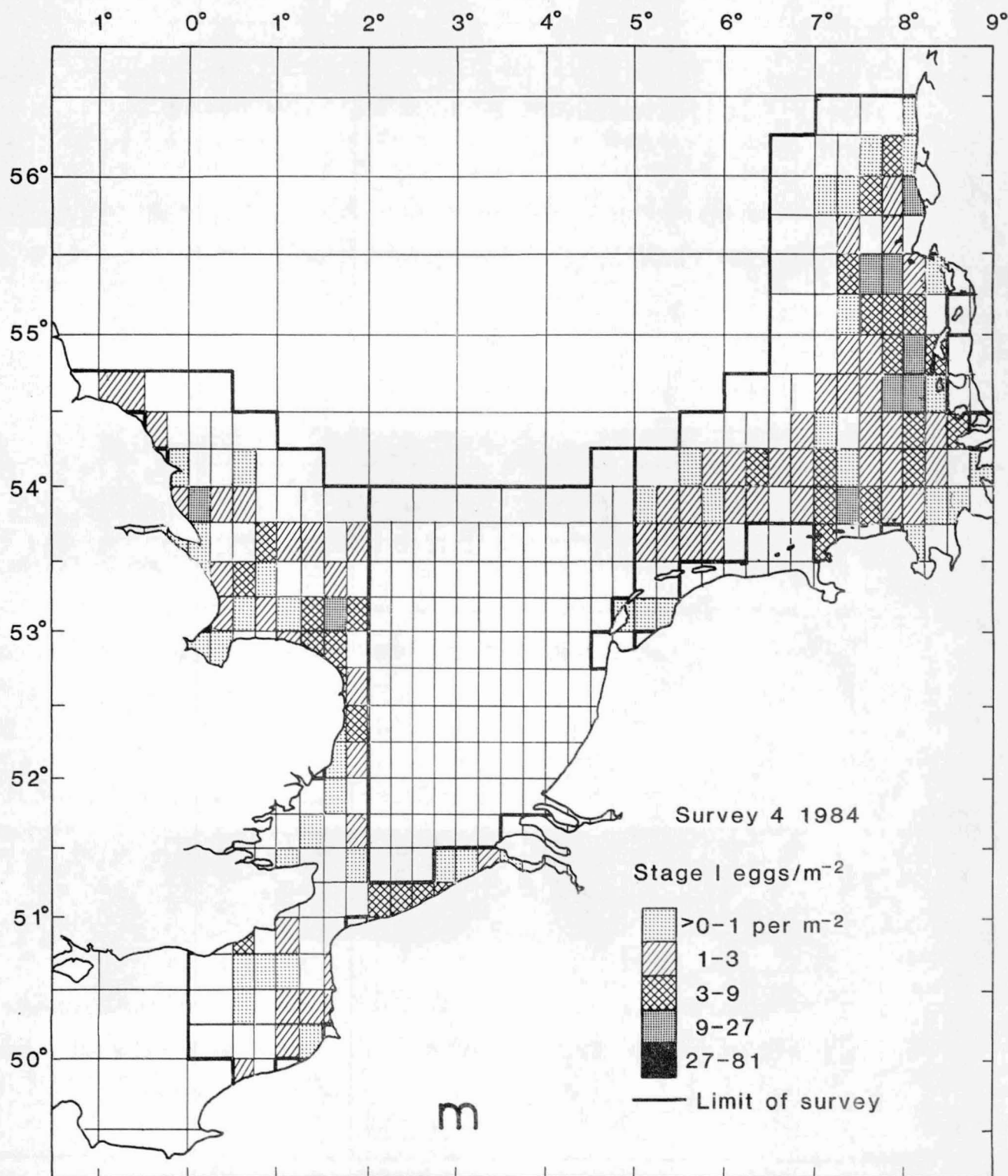


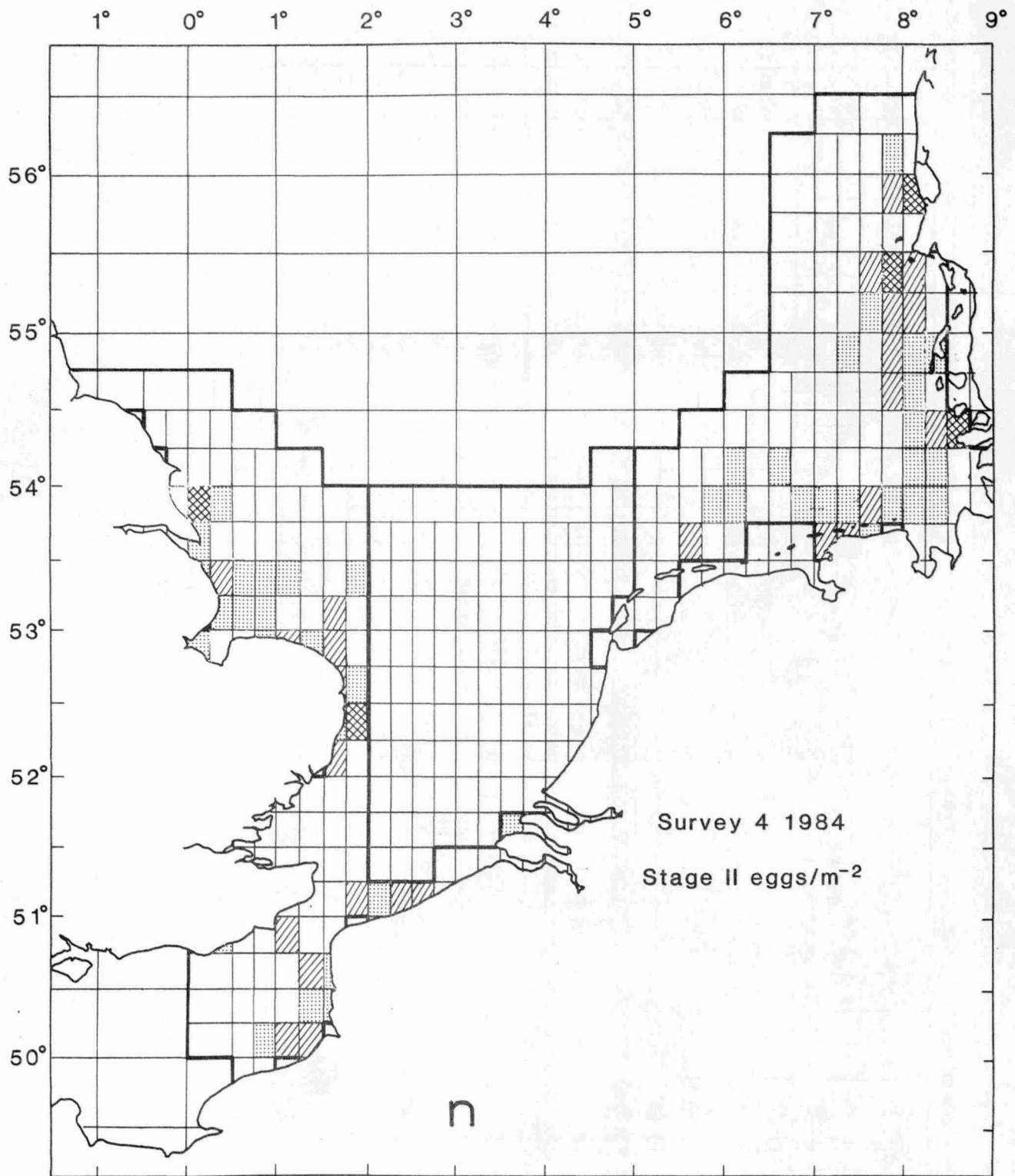


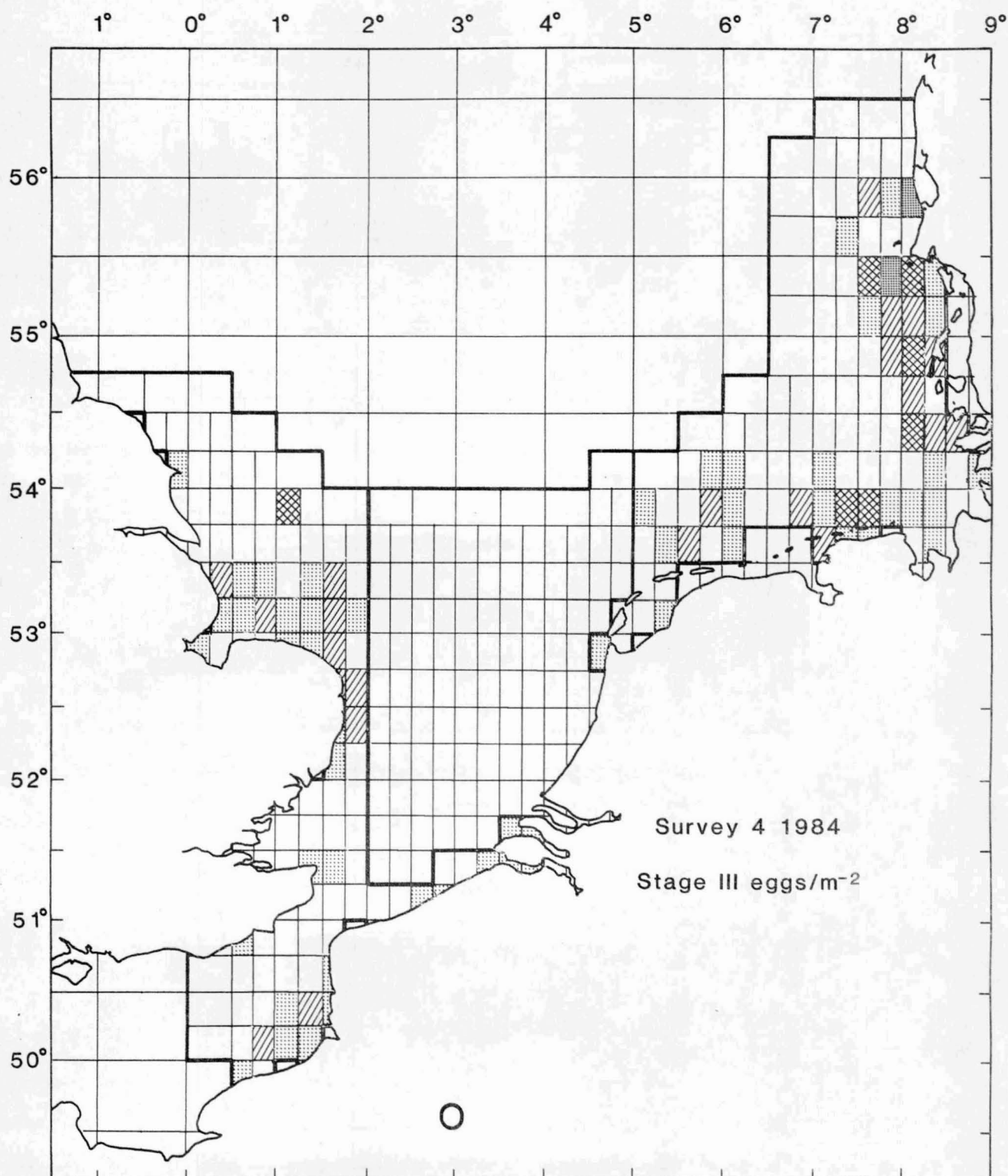


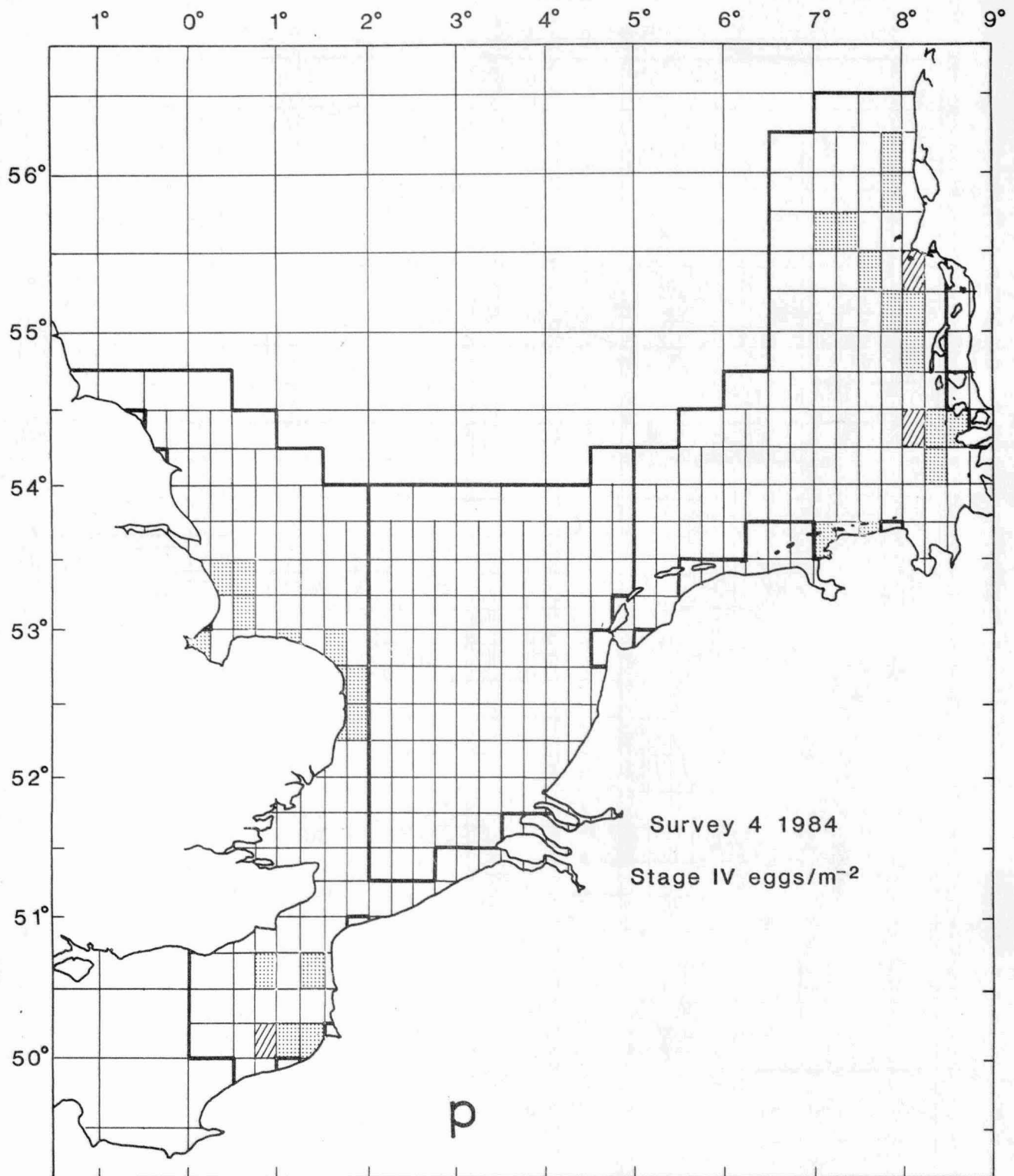
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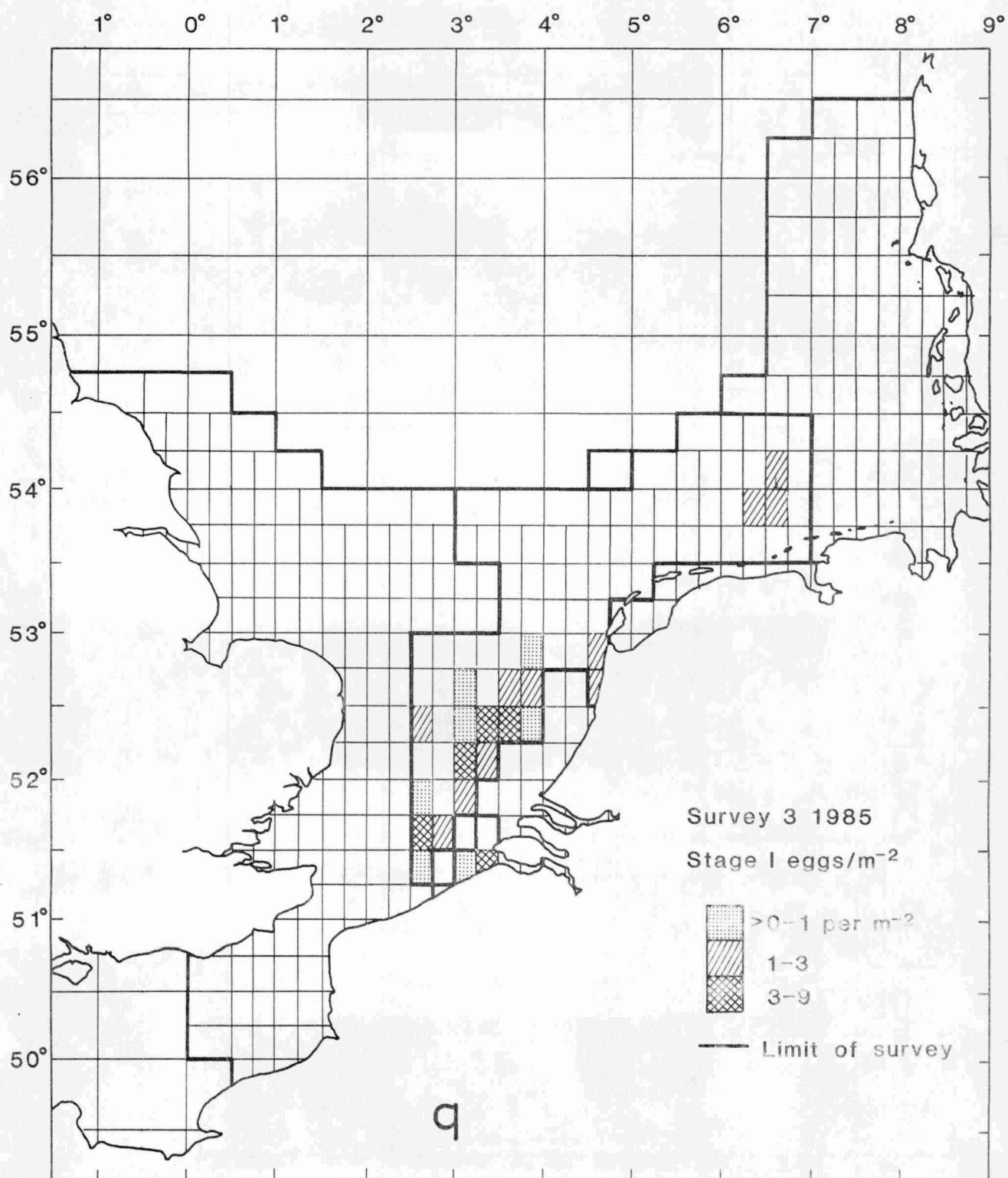


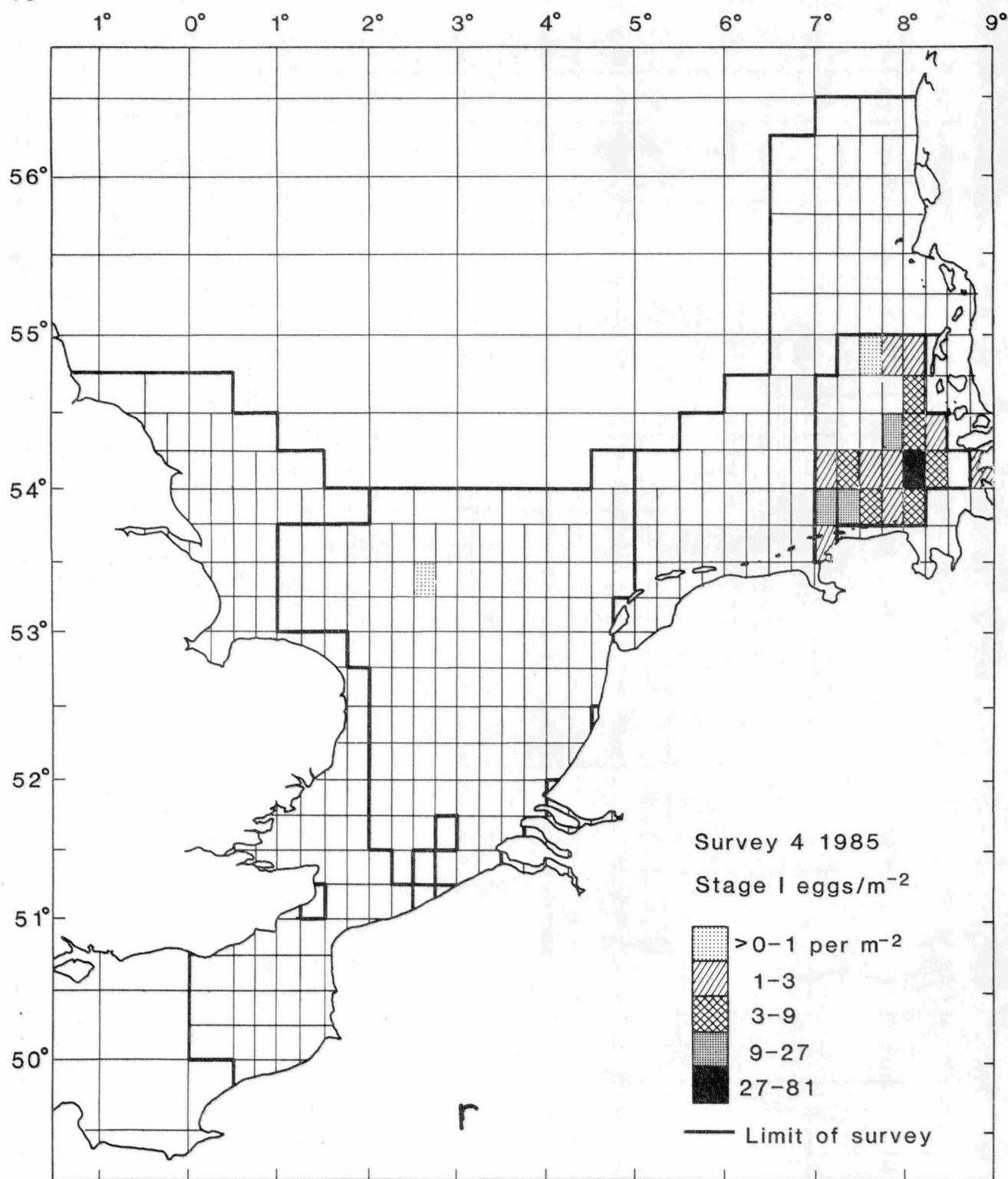












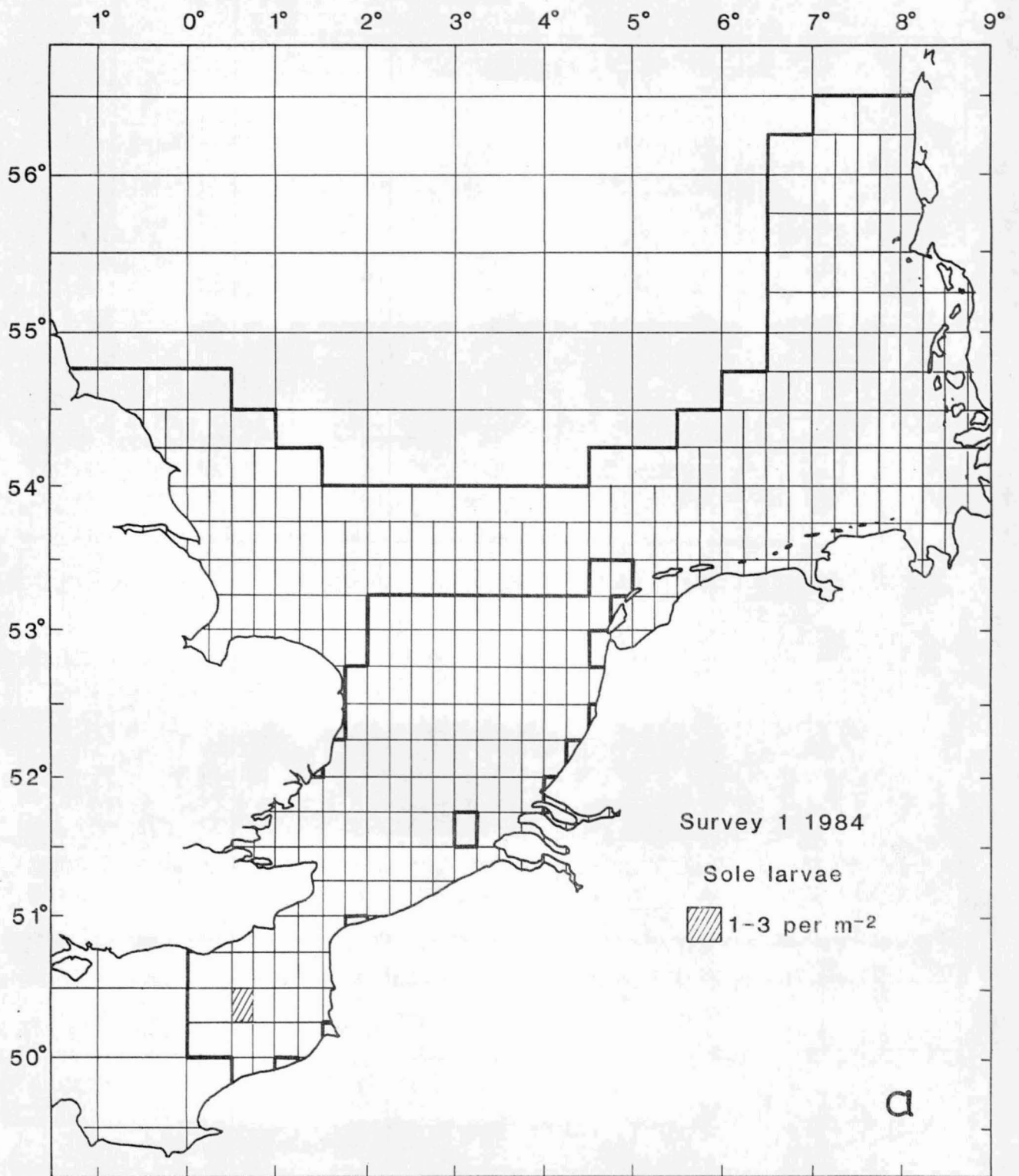
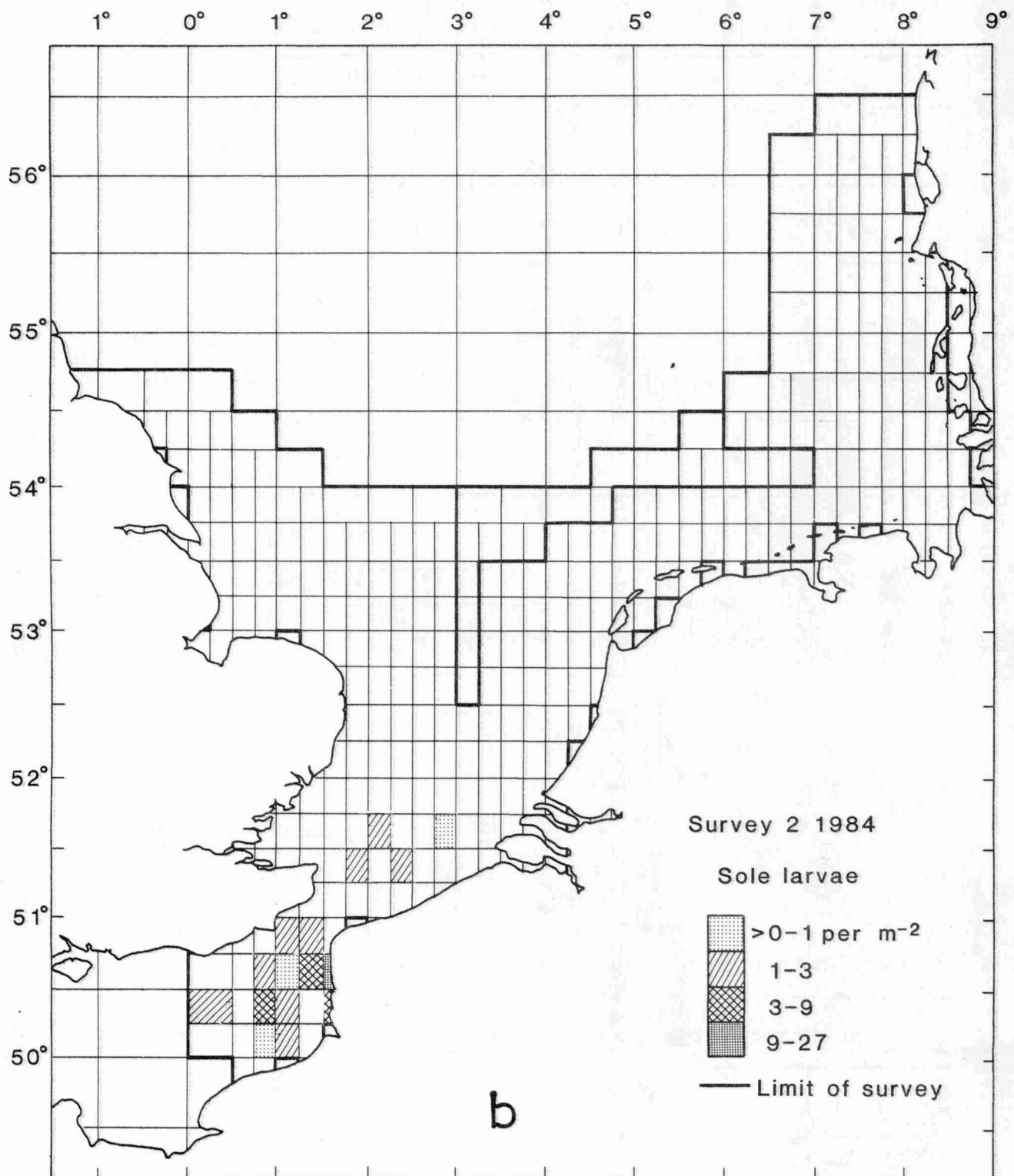
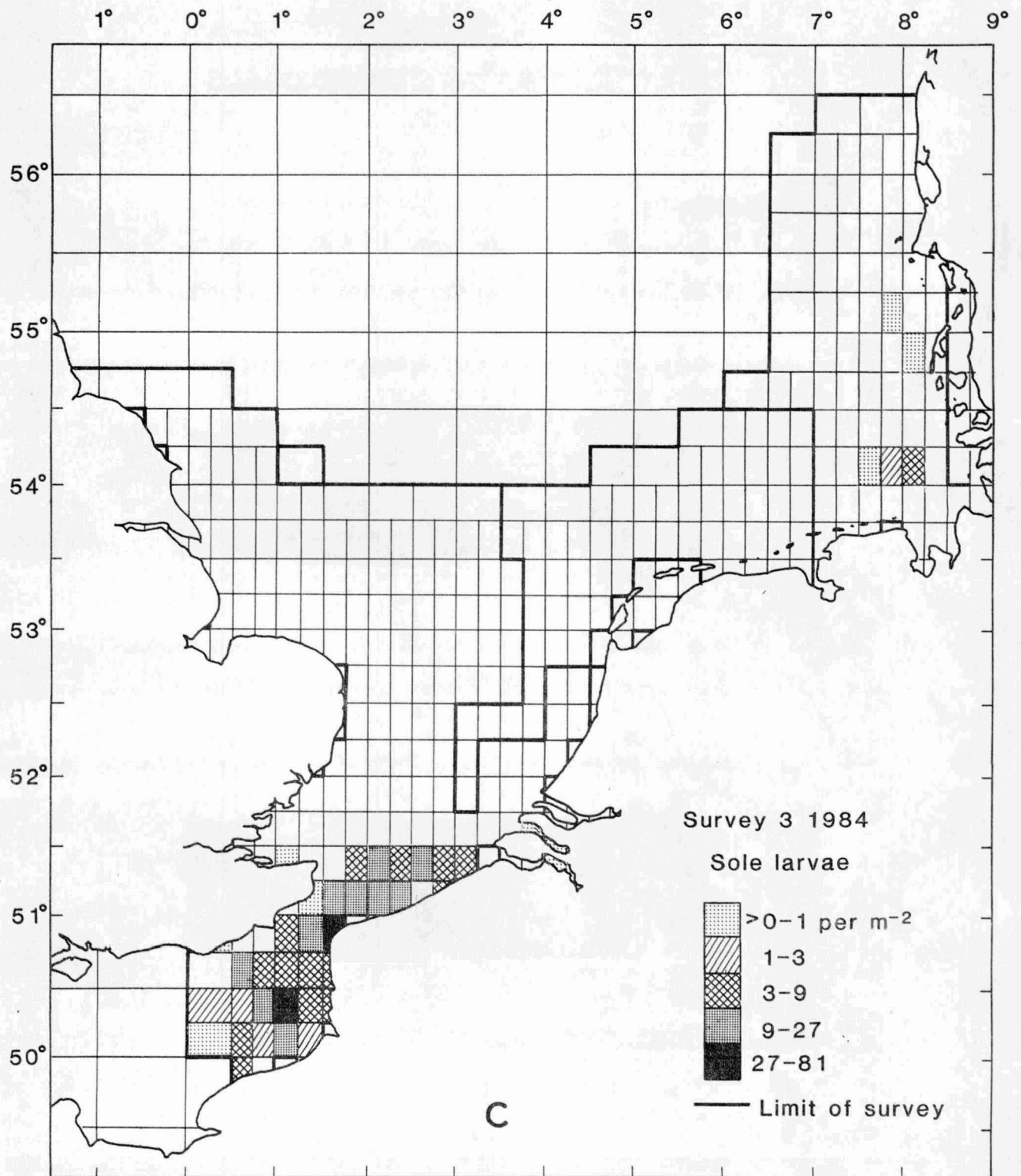
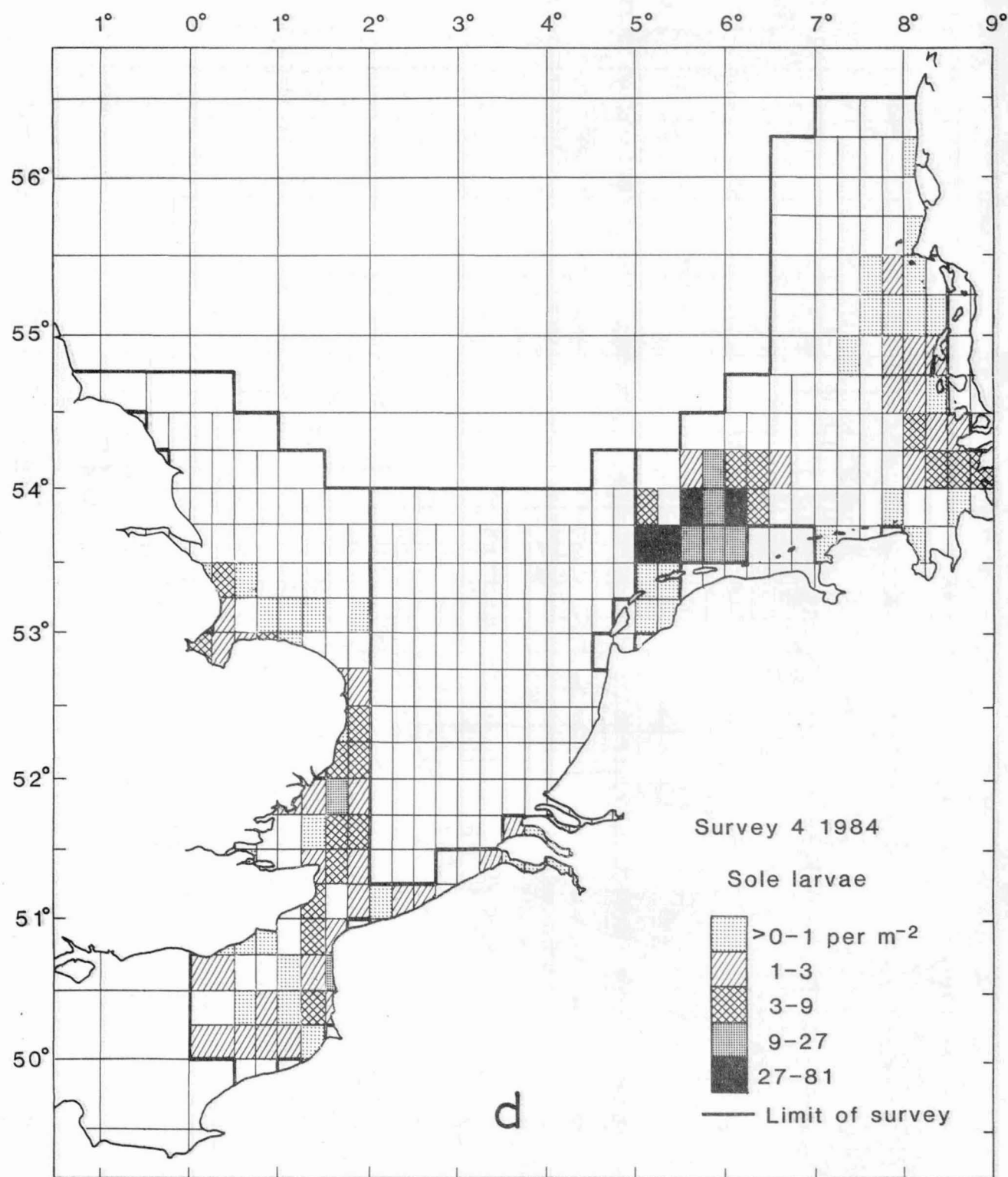


Figure 3.1.2 Abundance of sole larvae during the 1984 surveys.







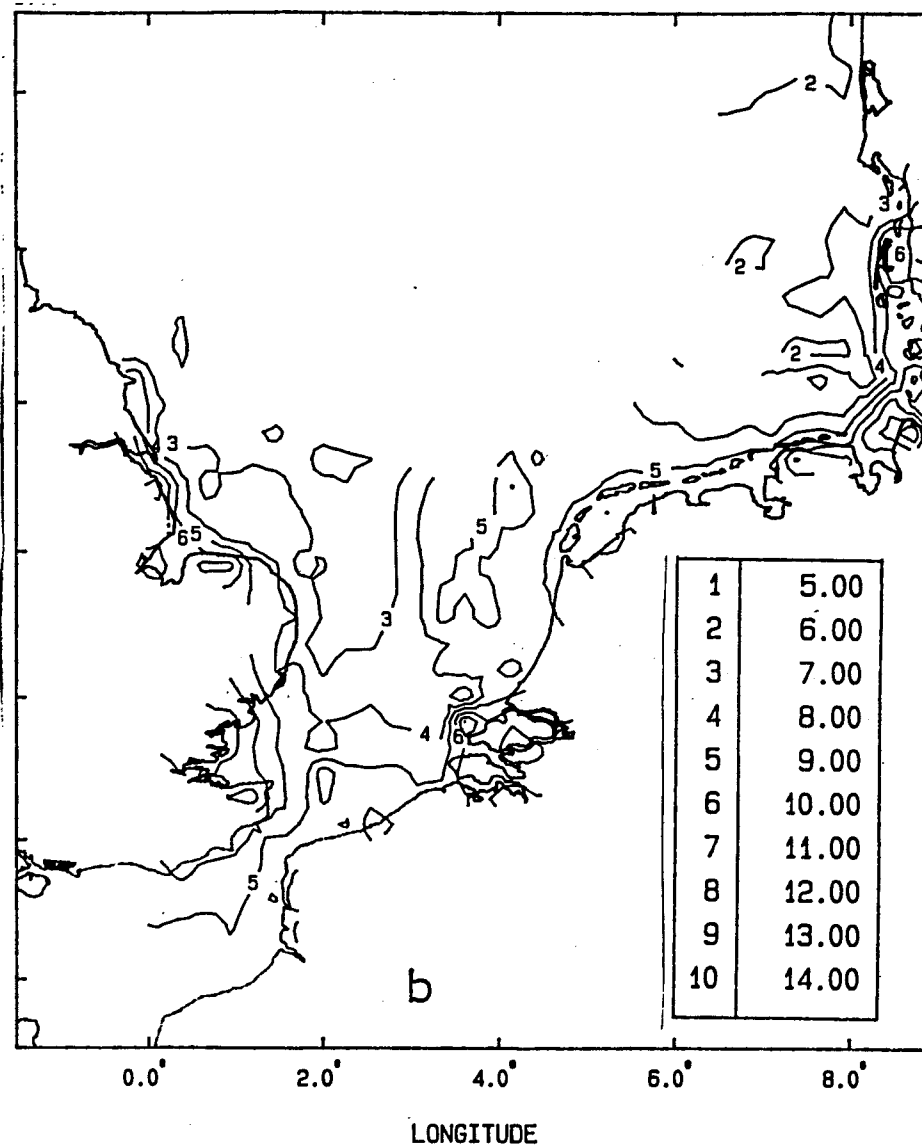
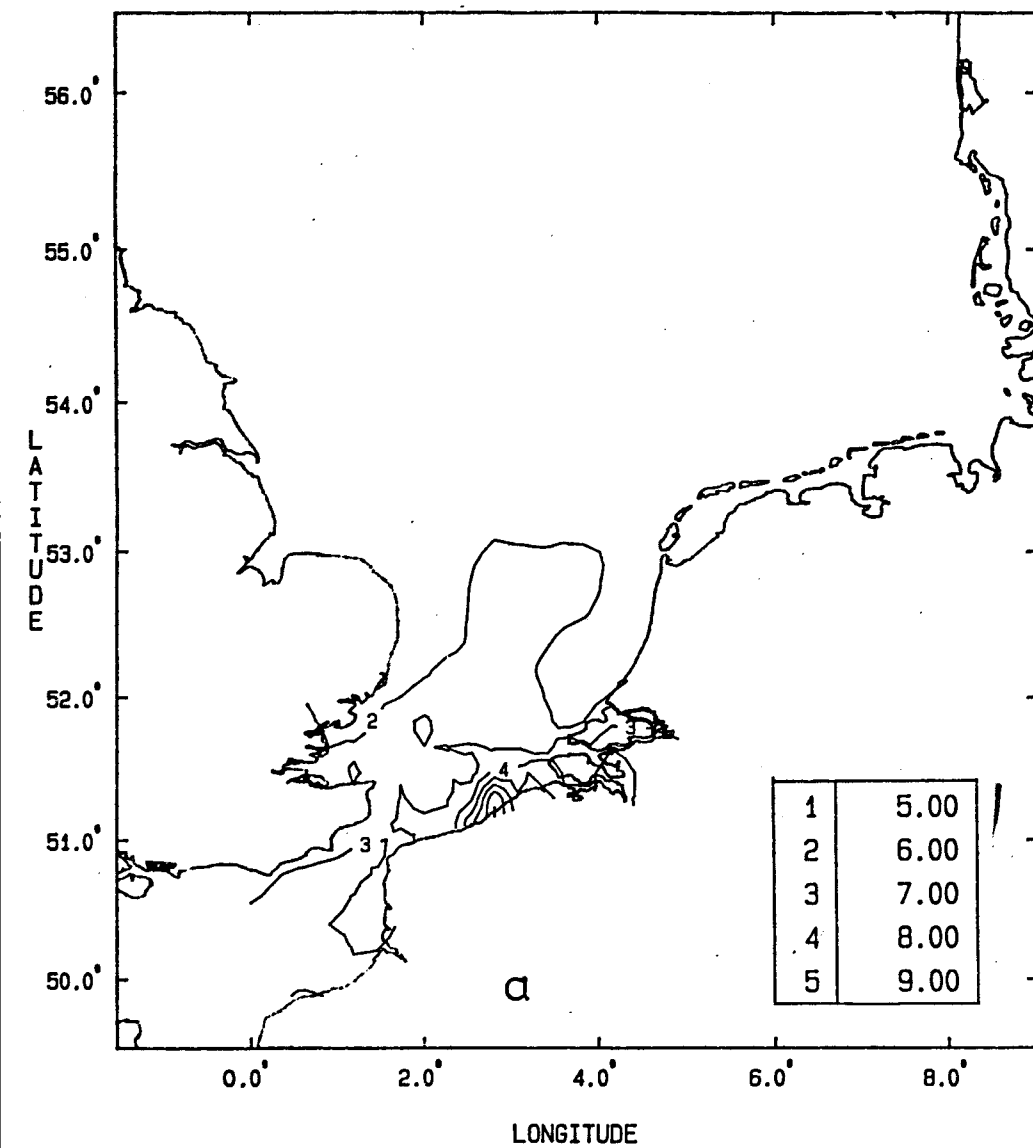
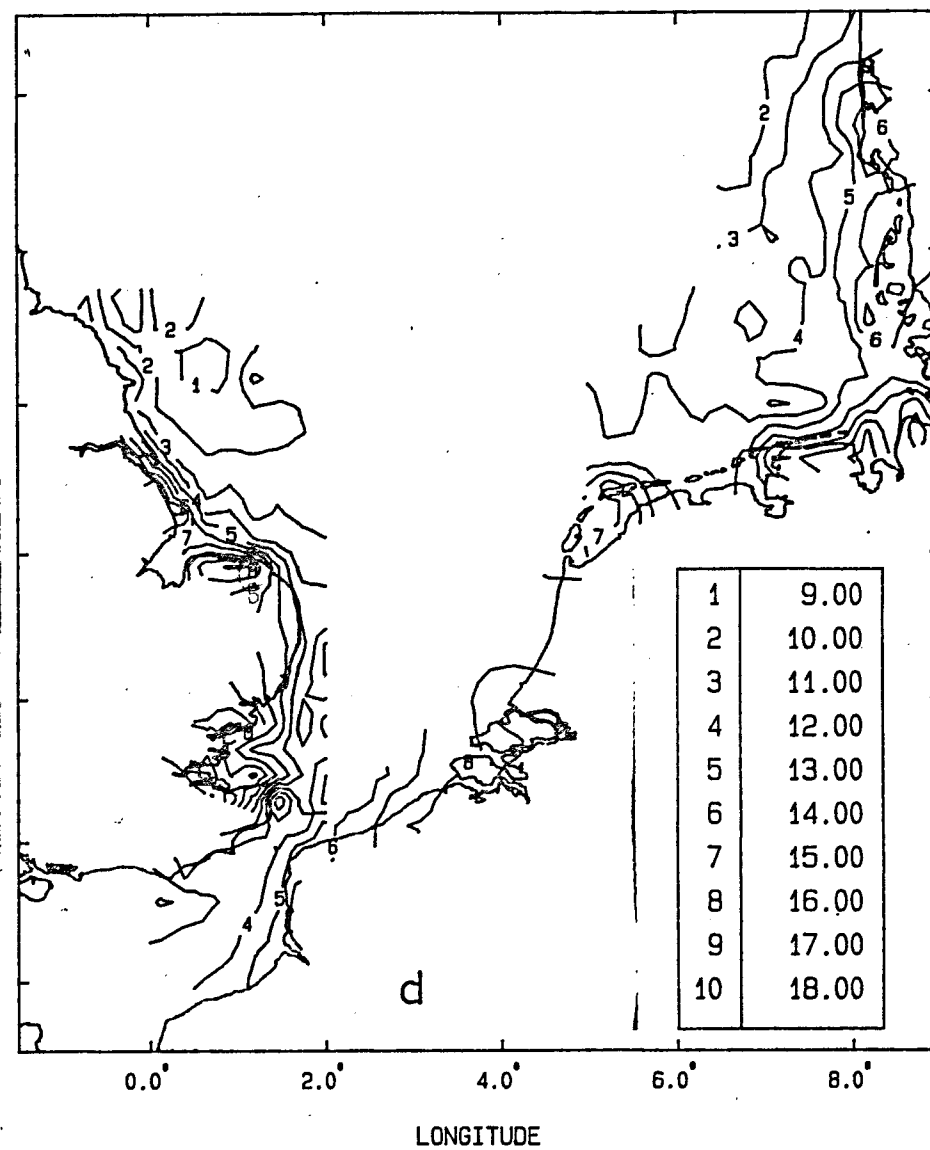
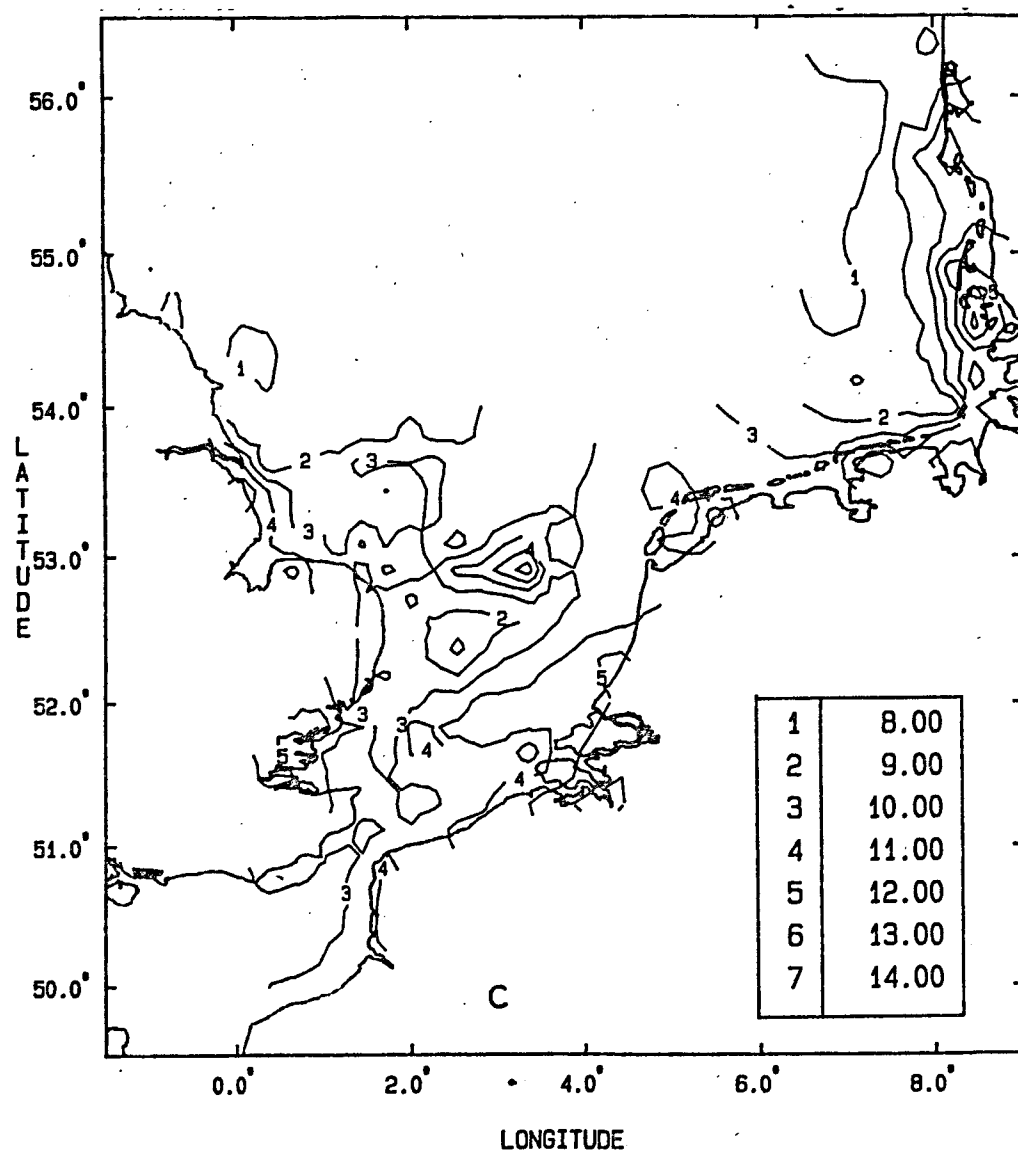


Figure 3.2.1a-d Contour diagrams of surface temperature (°C) during the 1984 surveys.



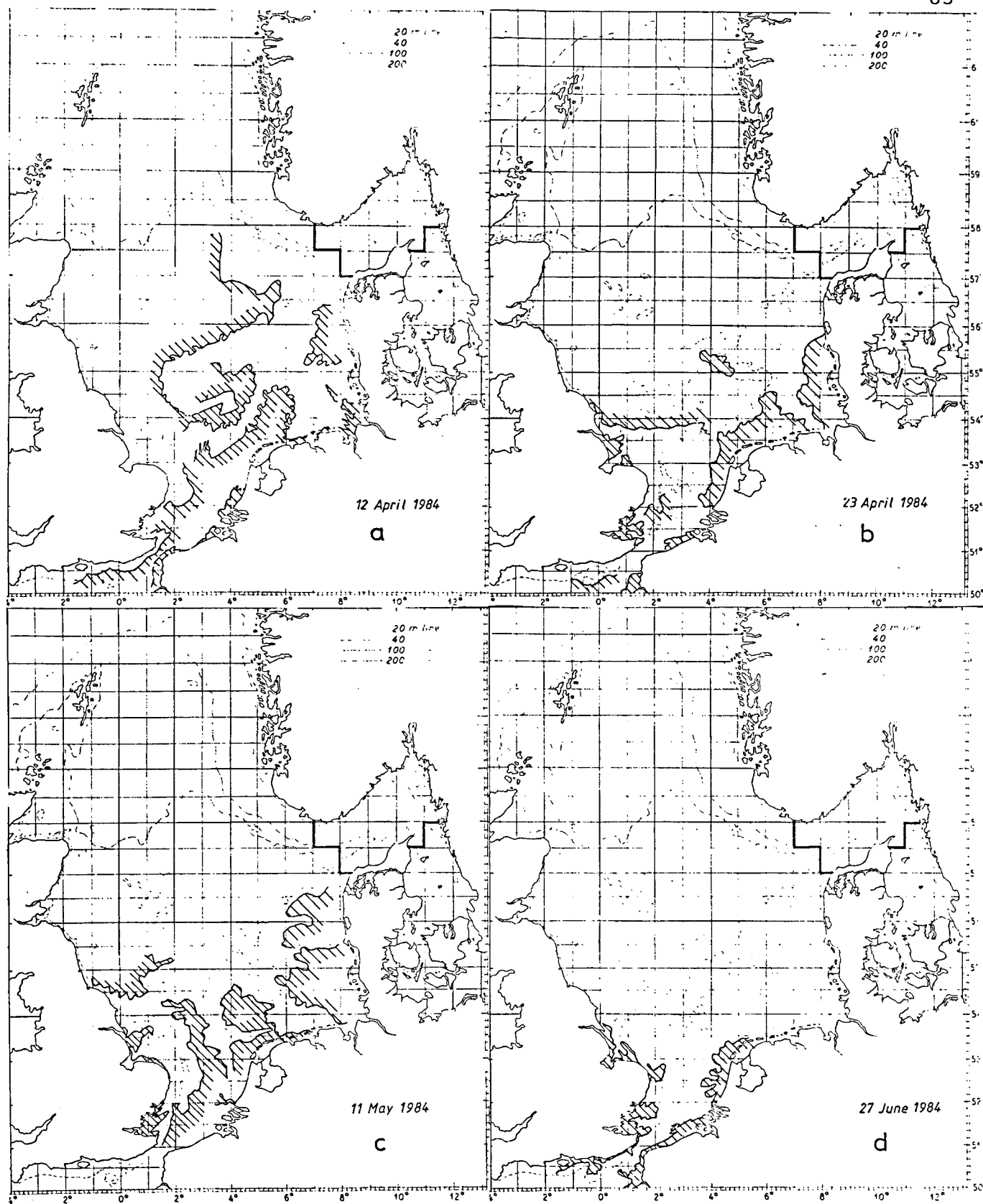


Figure 3.2.2a-d Summary of the position of thermal fronts based on infra-red images from the N-7 satellite.

Figure 3.2.3 Frequency distribution of samples by water depth for the 1984 survey.

Mean depth = 25.1 m

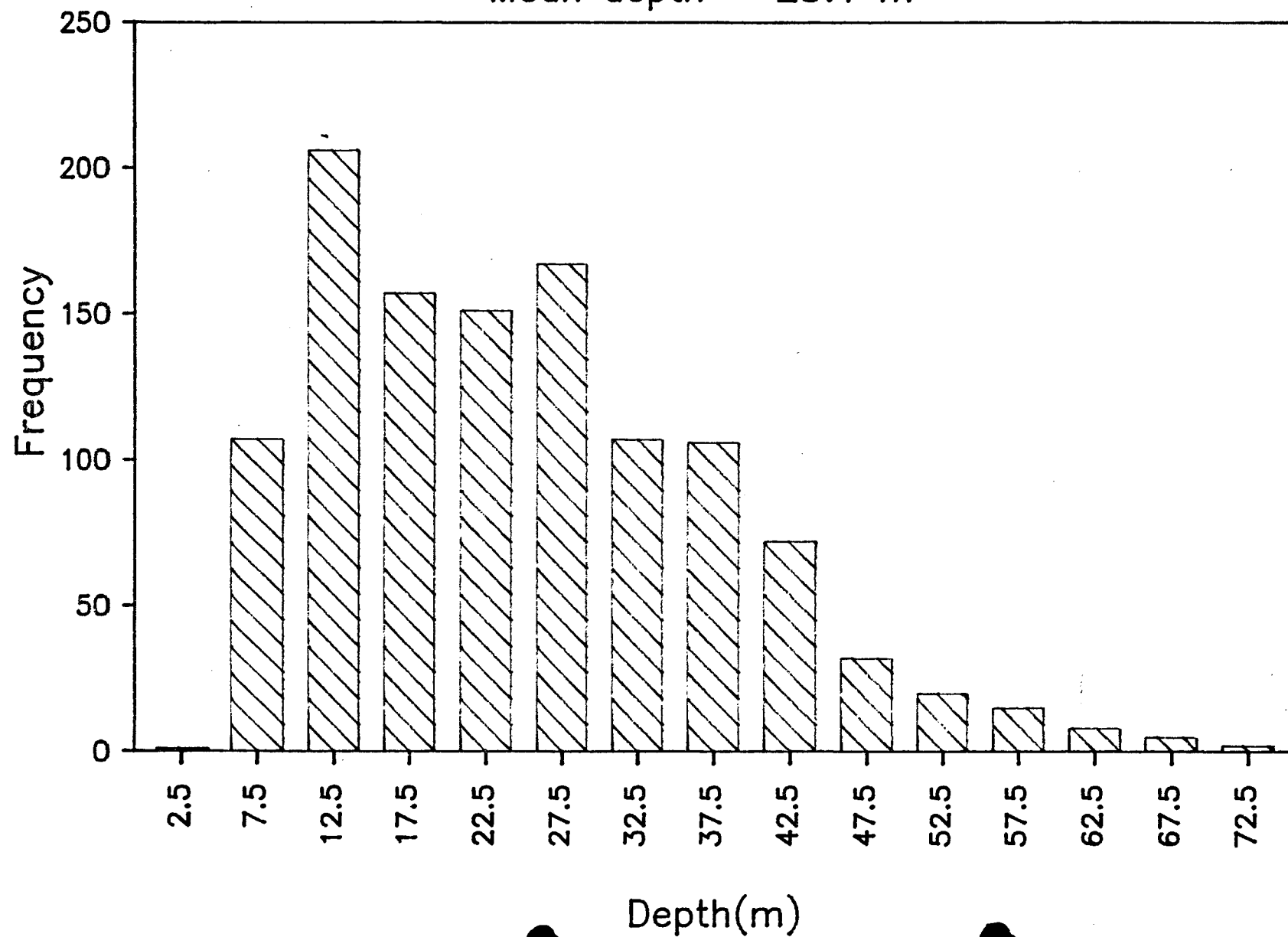
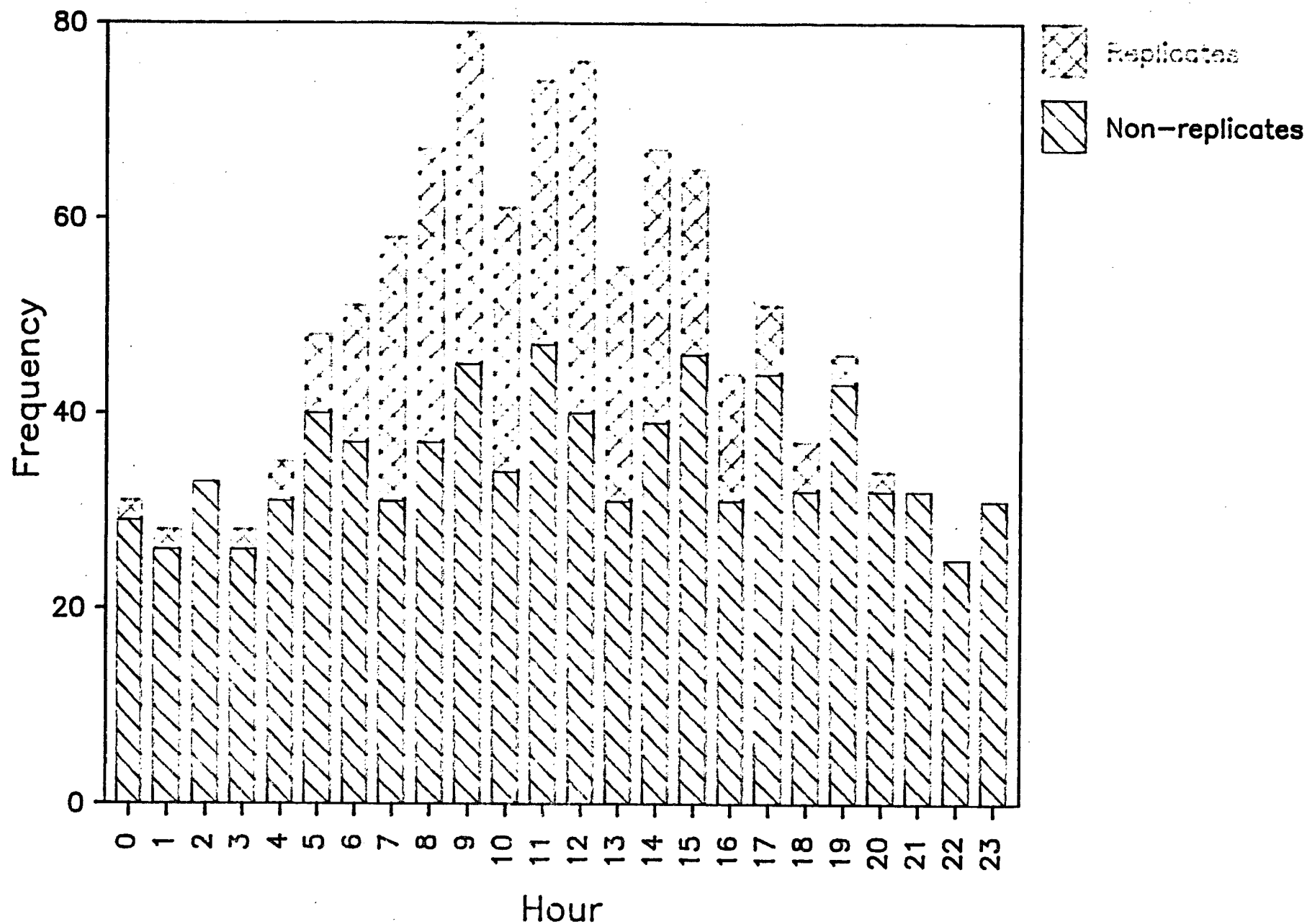


Figure 3.2.4 Frequency distribution of samples by time of day for the 1984 survey indicating separately the replicated samples (mainly in coastal and estuarine waters).



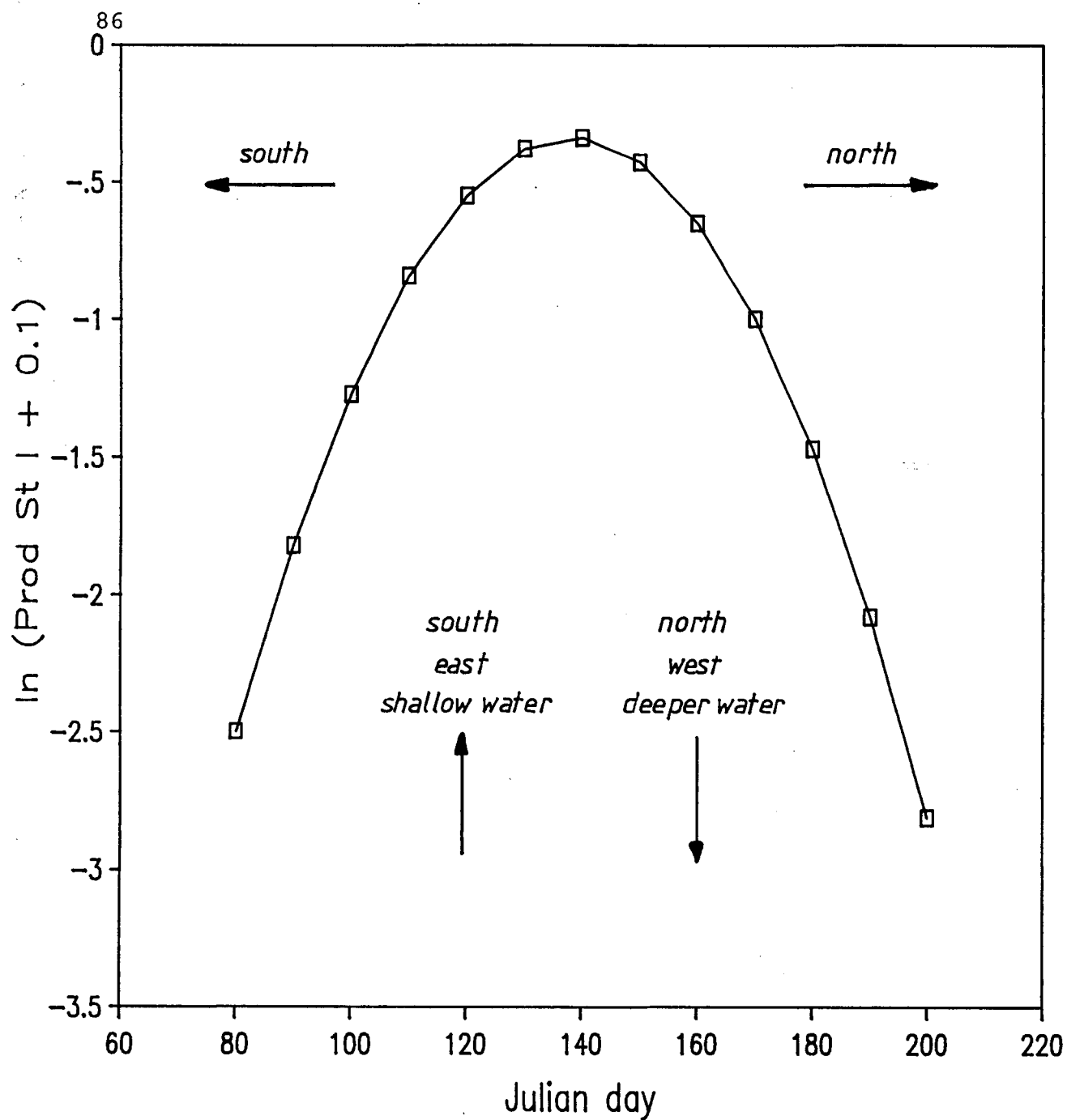


Figure 3.3.1 Quadratic function of $\text{DAY} + \text{DAY}^2$ fitted to \ln (production of Stage I eggs + 0.1) for the 1984 surveys.

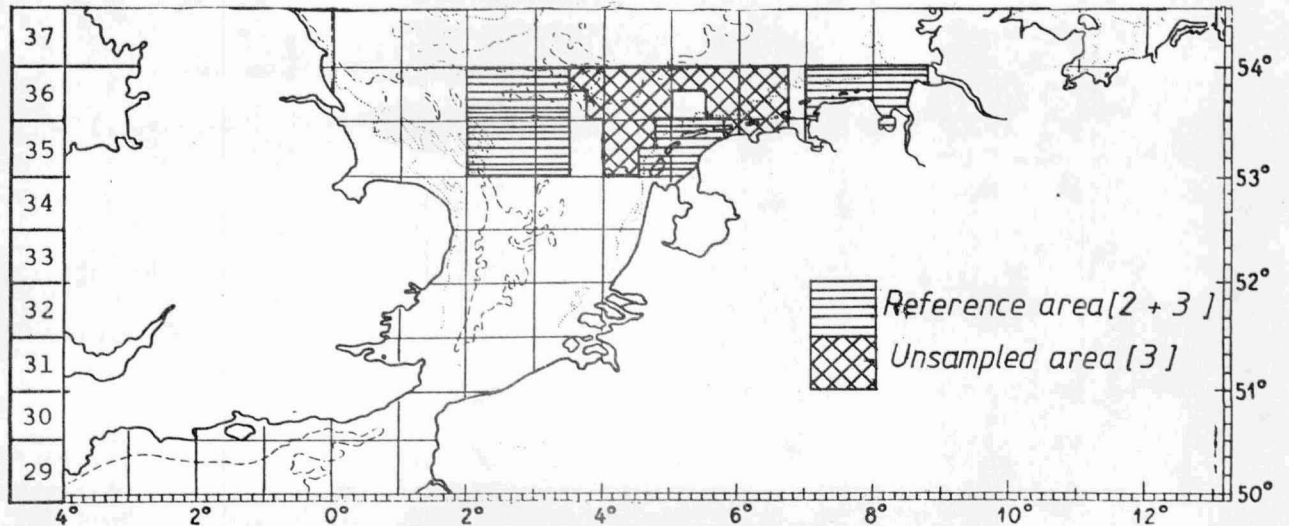


Figure 4.3.1 Chart to show the unsampled area on survey 3, 1984 and the areas used to estimate the missed production.

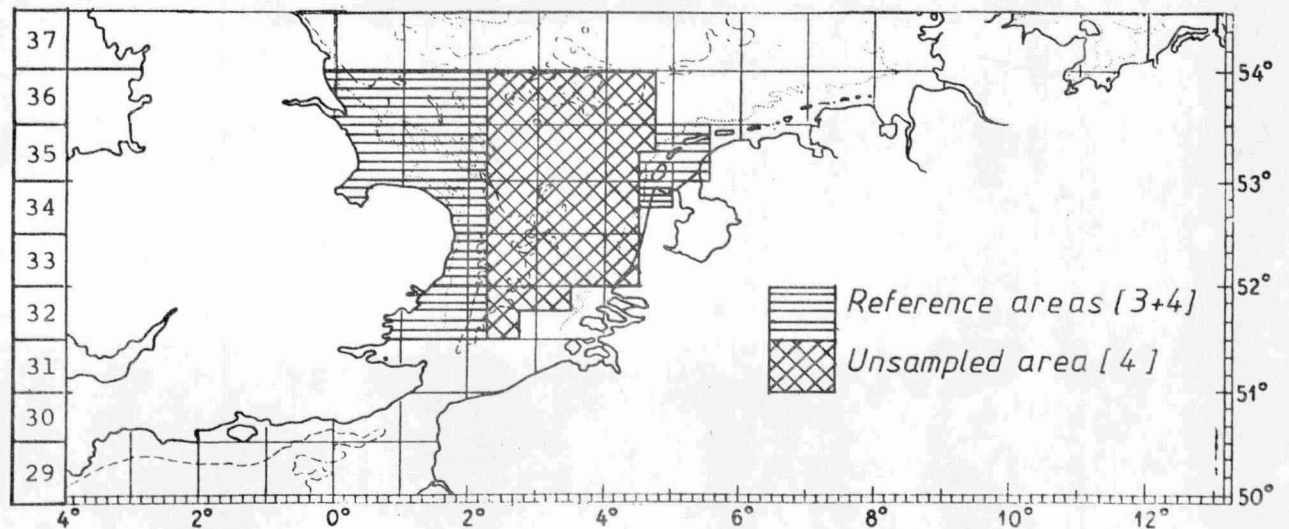


Figure 4.3.2 Chart to show the unsampled area on survey 4, 1984 and the areas used to estimate the missed production.

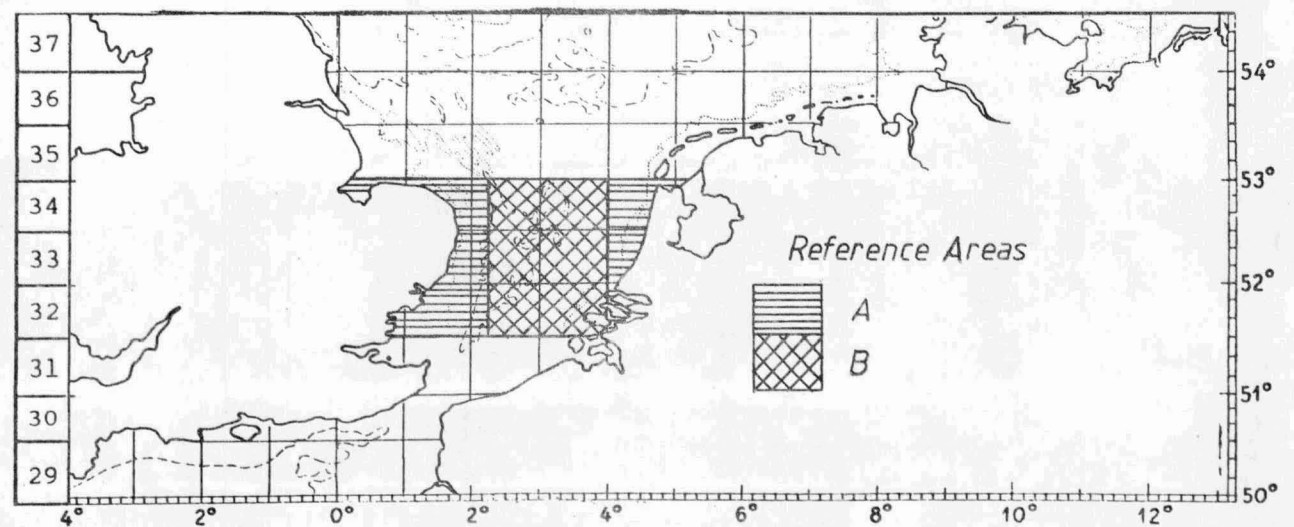


Figure 4.3.3 Chart to show the reference areas used to estimate the potential extrapolation error for unsampled areas.

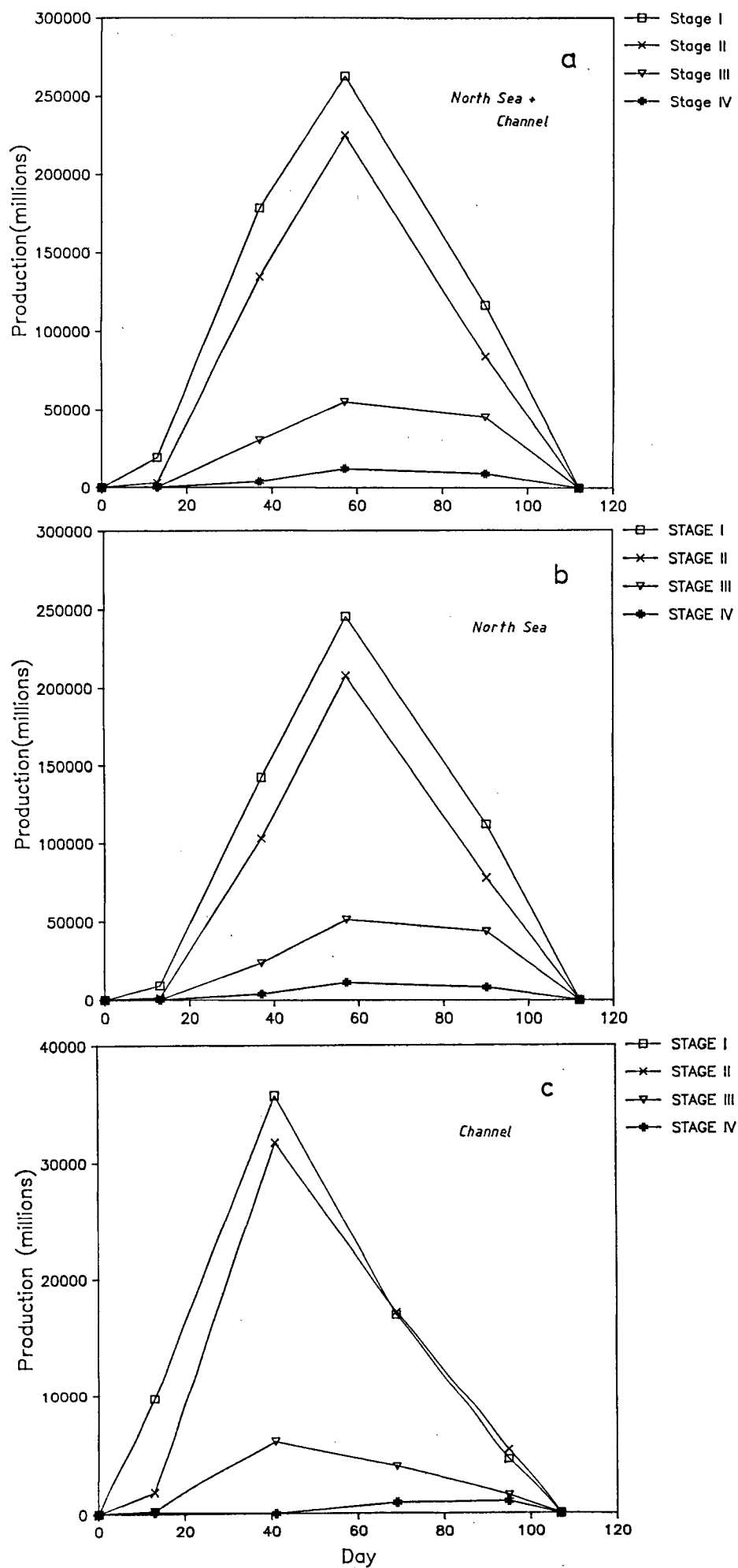


Figure 4.4.1a-c Production curves for each stage of sole eggs in the 1984 surveys for (a) the North Sea and Channel combined, (b) the North Sea only and (c) the eastern English Channel only.

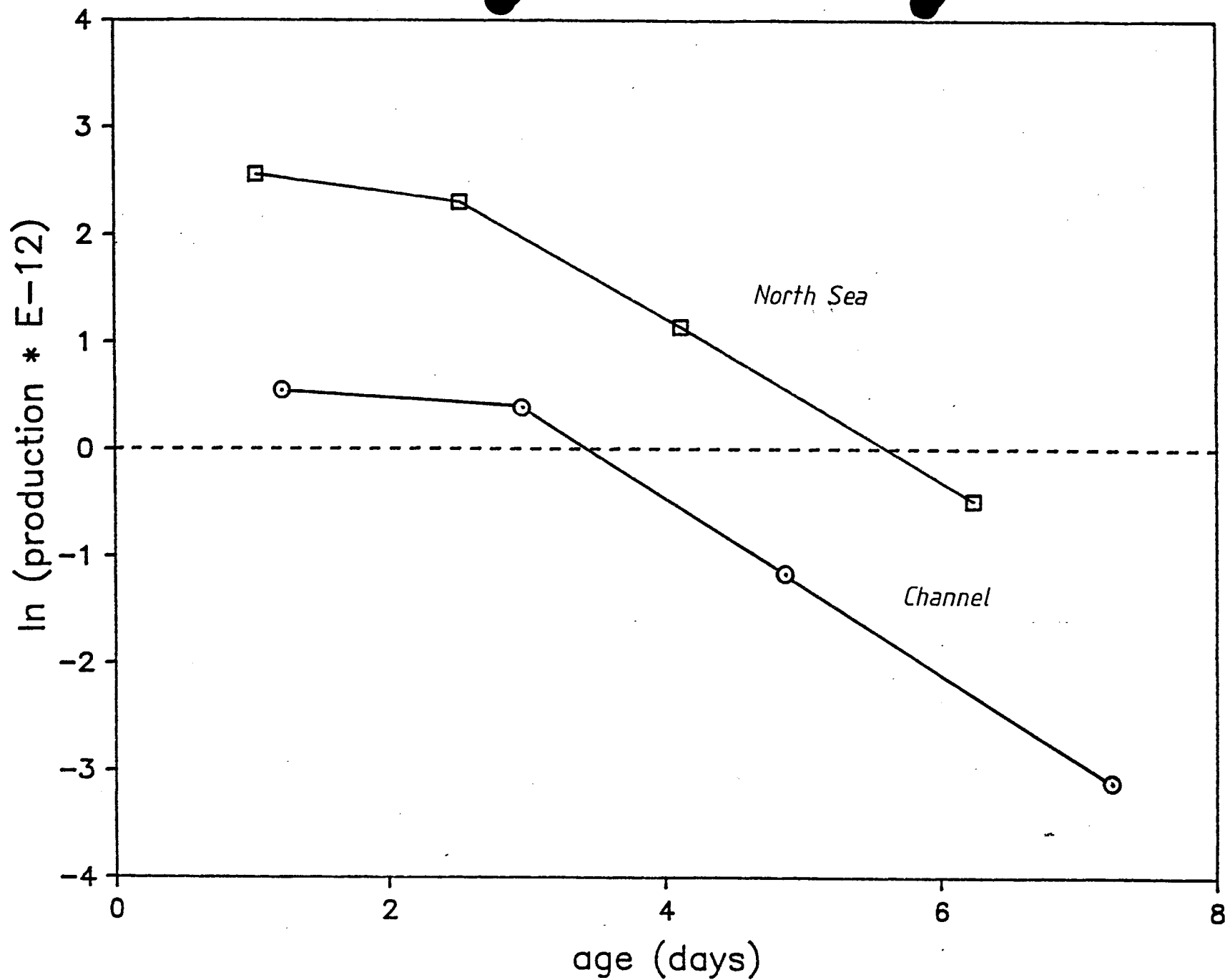


Figure 4.4.2 Survival curves for the 1984 survey showing the North Sea and eastern English Channel combined and separately.

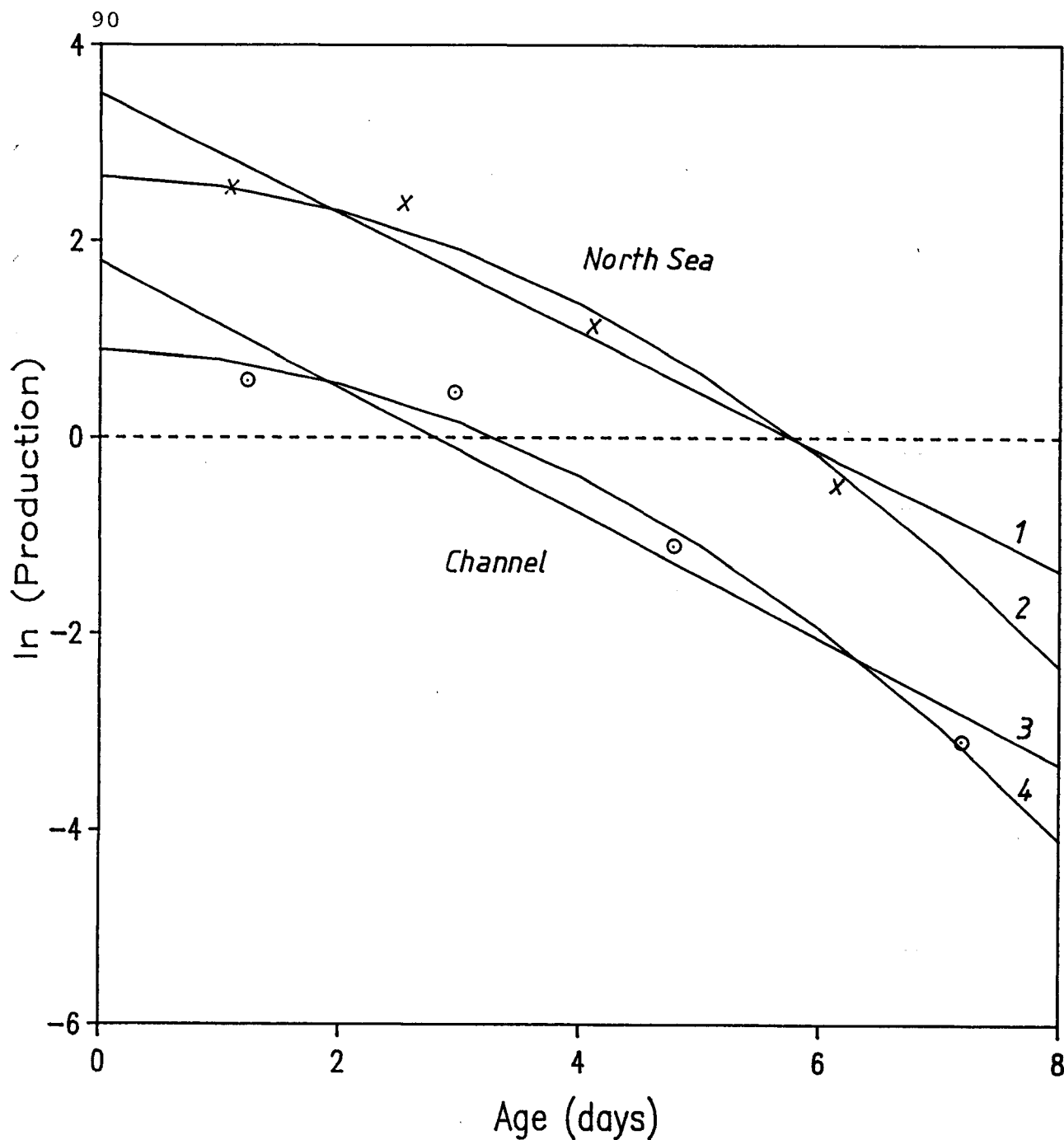


Figure 4.4.3 Survival curves for the 1984 survey showing the North Sea and Channel separately and the fitted linear and quadratic curves.

Equation 1: $Y = 3.493 - 0.607x$

2: $Y = 2.647 - 0.0218x - 0.0752x^2$

3: $Y = 1.788 - 0.6411x$

4: $Y = 0.890 - 0.0218x - 0.0752x^2$

(Models 1 and 3 were fitted independently, Models 2 and 4 were fitted with common coefficients to x and x^2).

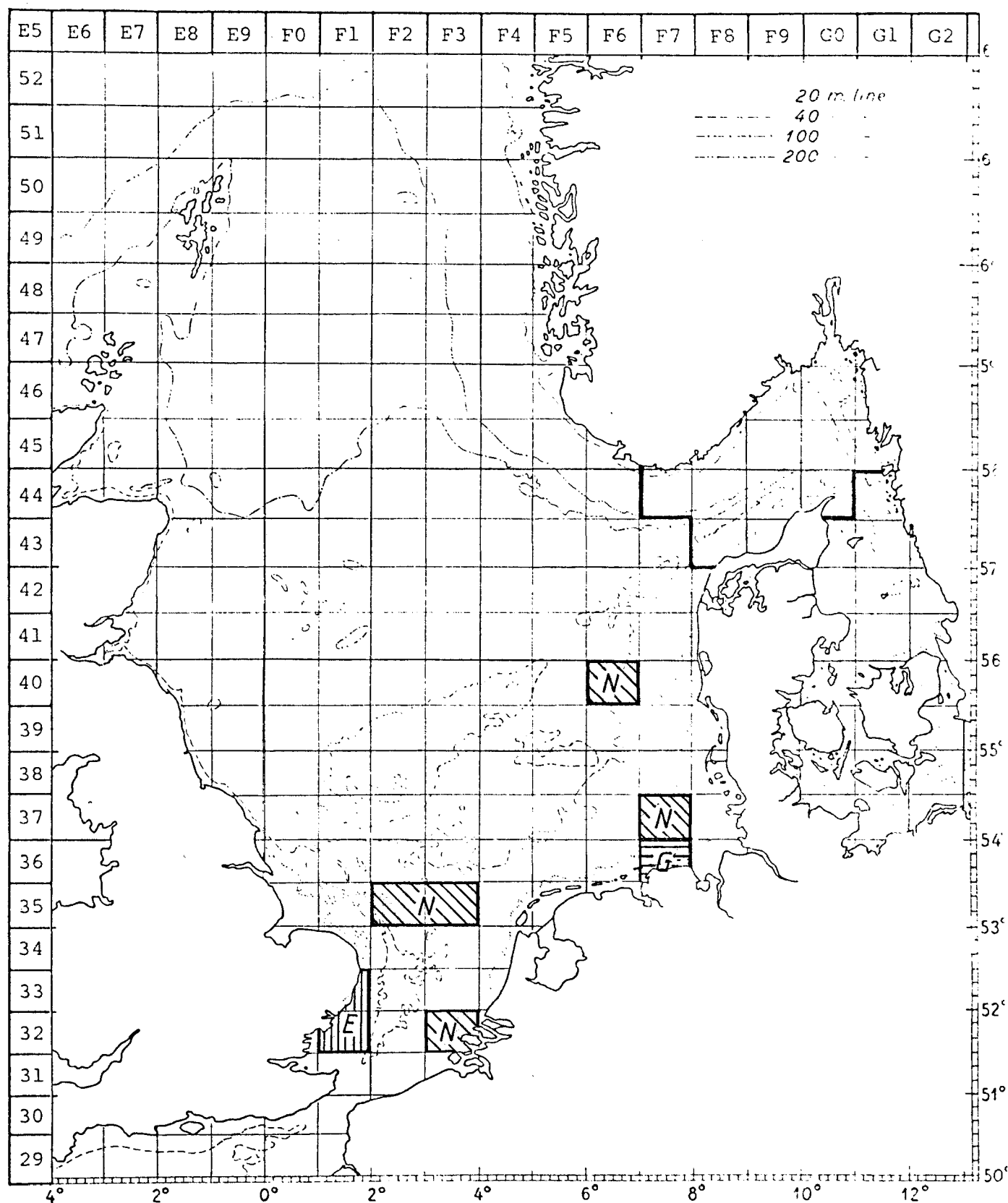
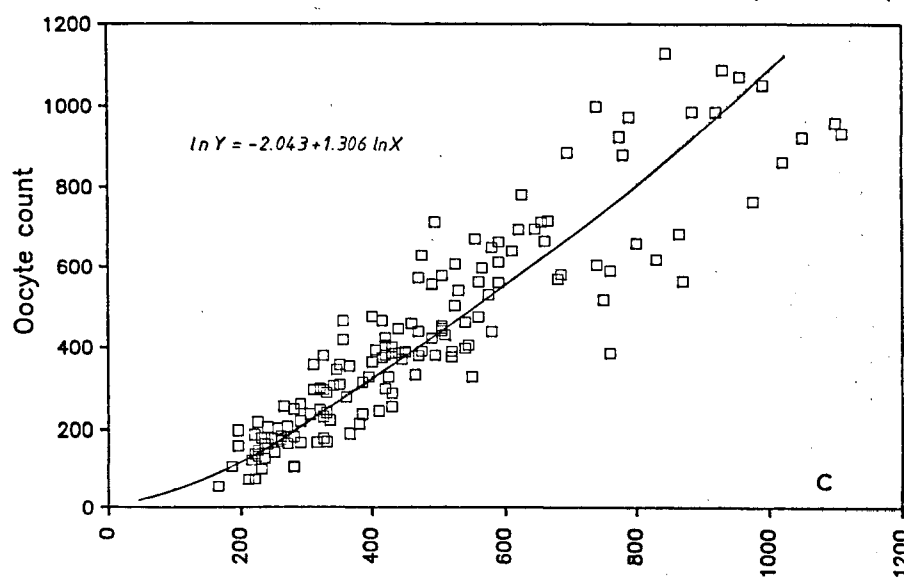
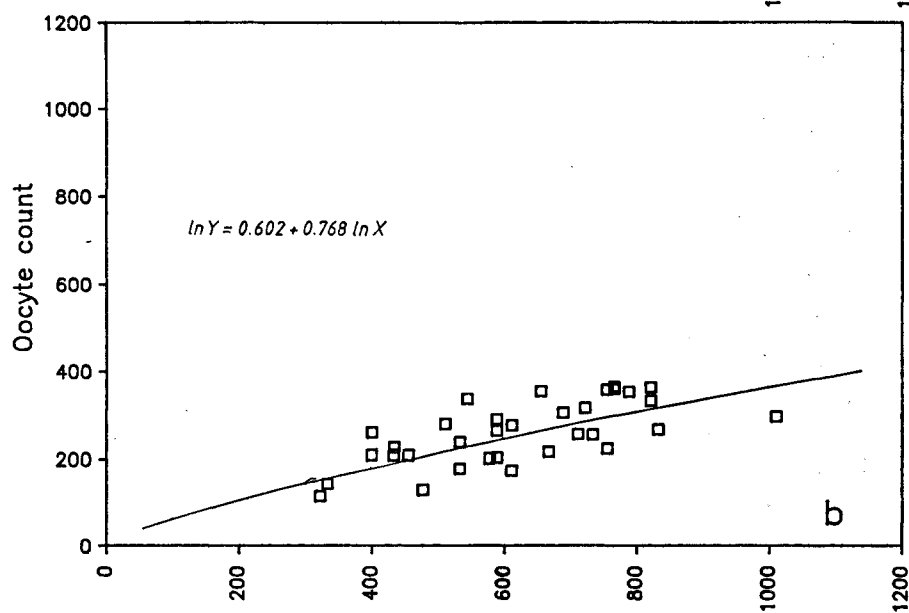
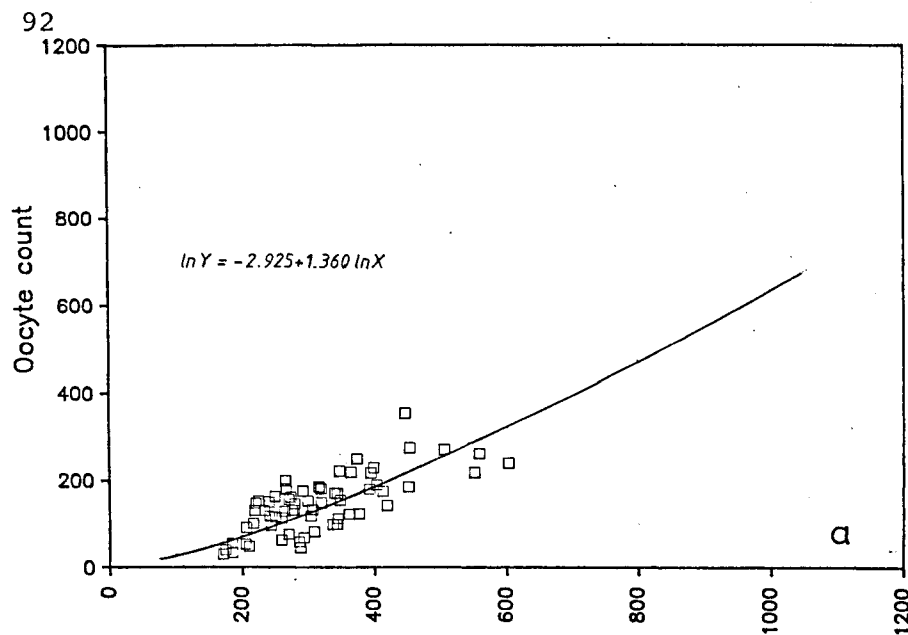


Figure 6.1.1 Origin of fecundity samples, E = England, N = Netherlands,
 G = Germany.



Total weight

Figure 6.2.1 Fecundity-total weight relationships for (a) English, (b) Dutch and (c) German samples.

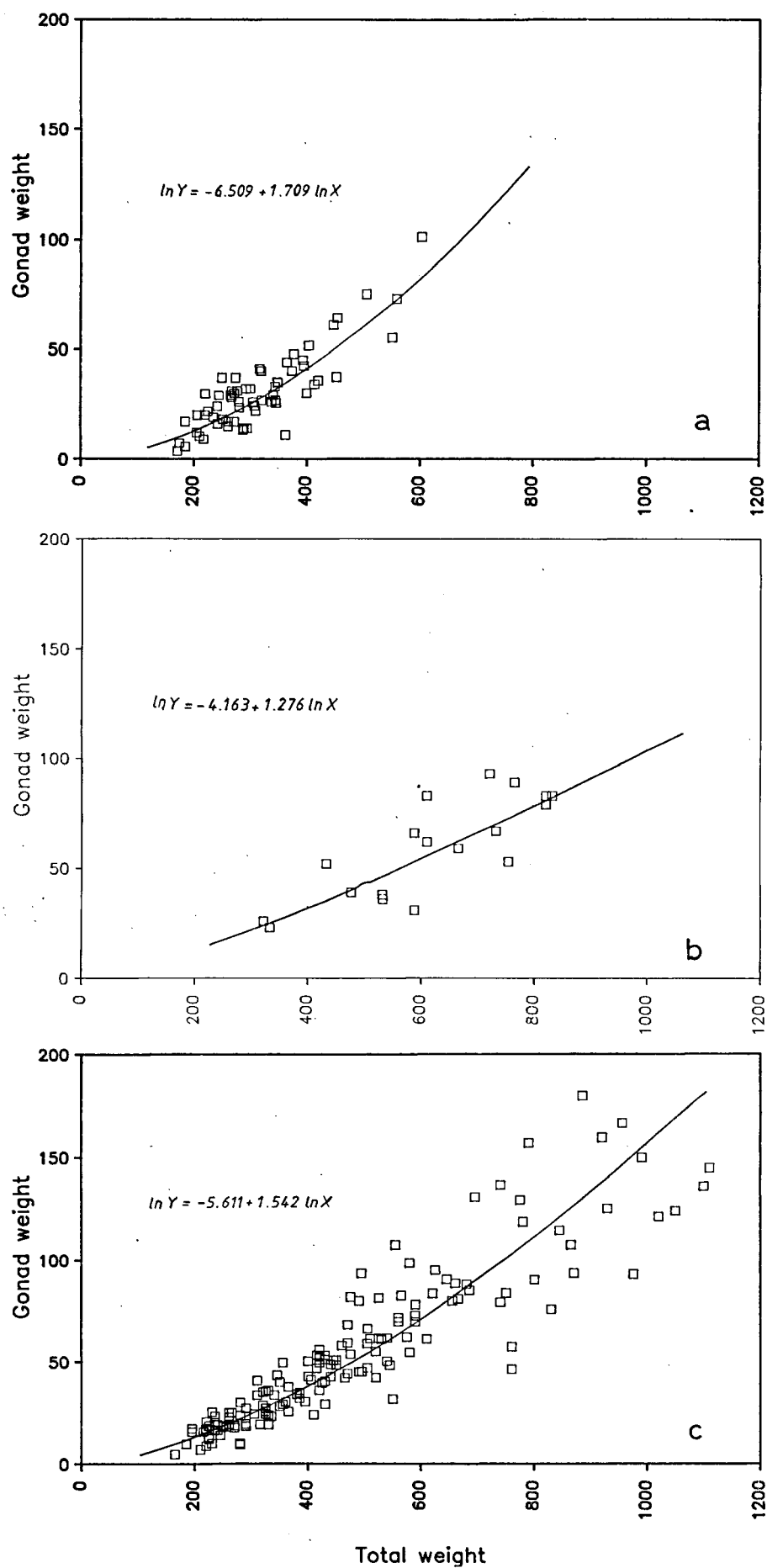


Figure 6.2.2 Gonad weight-total weight relationships for (a) English, (b) Dutch and (c) German samples.