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**THE RELATIONSHIP BETWEEN THE LOCATION OF WESTERN MACKEREL
SPAWNING, LARVAL DRIFT AND RECRUIT DISTRIBUTIONS:
A MODELLING STUDY**

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SUMMARY

Mackerel spawning distributions have changed over the last 20 years. From 1977-1995 there has been a progressive westerly shift in the distribution of spawning in May/June (peak spawning), with a resultant increase in the proportion of spawning west of the shelf break. Also during this time period there has been a marked increase in the proportion of spawning in the north of the spawning area. This shift occurred most obviously between the surveys carried out in 1986 and 1989. At the same time it is shown that there has been a northerly shift in the distribution of first winter juveniles. These observations are derived from data collected on the ICES coordinated winter bottom trawl surveys.

This study used data on mackerel egg distributions during May, derived from the ICES triennial mackerel egg surveys as input to the NORWECOM transport model, using real weather fields. The outputs from the model indicated that most eggs and larvae could expect to be transported south after spawning and that there had been no significant change in this transport pattern during the period studied. The combination of more northerly spawning and the prevailing transport pattern may explain, in part, the increase in the recruit population in the northern nursery areas. It is concluded that passive transport can explain the juvenile distribution in some areas, but that active migration must also play a role in the area of the Celtic Sea.

The interactions between the modelled transport patterns and the real egg distribution data are discussed with reference to these topics and to the potential survival of larvae in the first weeks after hatching.

INTRODUCTION

Spawning of western mackerel occurs mainly along or very close to the shelf-edge from the Bay of Biscay to west of Scotland (Anon, 1996a) with peak spawning in the months May-June. Variations in the poleward flow of the slope current (Fig. 8) offers a potential mechanism by which inter annual changes in the distribution of juveniles might occur.

Work in progress under the SEFOS project¹ and summarised in this paper has indicated that marked changes in the distributions of stage I mackerel eggs and first year juveniles (approximately six month old fish) occurred simultaneously - between 1986 and 1989 - and might, therefore, be inter related. The assumption made in this study is that if passive transport is a factor in determining juvenile distribution it is likely to be of most importance during the first month of life, through the egg stage (approximately one week) and subsequent early development stages (another three weeks) until a more actively swimming phase is reached. The possible effect of diel vertical migration during the larval phase as a means of influencing destination is not considered in this study. Our starting hypothesis is that changes in the distribution of juveniles may be influenced either by changes in the pattern of circulation itself, eg changes in strength and direction of the slope current and/or by changes in the distribution of spawning in relation to this circulation. In the latter case relatively small changes in distribution relative to the slope current could theoretically result in substantially different distributions of the products of spawning after one months transport even with no interannual variation in circulation.

The aims of this study were:

- to document the changes in distribution of mackerel spawning and first winter juveniles in the western area.
- to investigate whether observed changes in the distribution of first winter mackerel juveniles could be accounted for by changes in circulation at the shelf edge (as modelled by the NORWECOM transport model) in the first month after spawning.
- to investigate the possible effect of distributional changes in spawning on subsequent nursery area.
- to evaluate the influence of passive and active transport and other relevant factors in determining the distribution of first winter juveniles.

With regard to the last objective, changes in the distribution of spawning and the way this interacts with circulation during the early life history stages, before mackerel are able to swim actively, may affect survival. Differential survival over different parts of the spawning area may be one of the relevant factors determining juvenile distribution. In the western spawning area it has frequently been observed during the egg surveys that crustacean zooplankton, the main food item of mackerel at this time of year, are abundant at the shelf edge and on the shelf while in the open sea areas to the west they are scarce and conditions desert-like. A possible hypothesis arising from such observations is that in years when spawning is more westerly or where the products of spawning are transported to the west survival will be poorer and the converse true when distribution and transport are more easterly. This hypothesis is briefly investigated in this report.

¹Shelf Edge Fisheries Oceanographic Study - An EC AIR programme supported project

MATERIALS AND METHODS

Egg Distributions

All egg data were obtained from the ICES triennial western mackerel egg surveys.

To quantify changes in the distribution of spawning over the period of the egg surveys the mean distributions of stage I mackerel eggs/m²/d⁻¹ per ½ degree rectangle at peak spawning time (May/June) were plotted for each survey year. Data were aggregated into four north/south strata each of which were further subdivided into strata east and west of the 200 m contour (Fig. 1).

To investigate transport of eggs from their point of origin to their destination after one month, egg data from the month closest to the peak and mid point of spawning (May) were selected. There have been seven triennial ICES egg surveys since their commencement in 1977, however in this study only those from the years 1980-1992 have been used because in 1977 there were no juvenile distribution data with which to compare the results, while in 1995 neither the juvenile data nor the transport data are yet available.

The input parameter for the transport model is the arithmetic mean number of stage I eggs below a square metre of surface per day, taken in the centre of sampled ½ degree x ½ degree rectangles (Figs 7a-e). Interpolated values from unsampled rectangles shown in these figures were not used in the model simulations. The egg distributions give a very close approximation to the actual distribution of spawning since the duration of this stage is very short, less than 48 h at ambient temperatures (Lockwood *et al.*, 1981). The start and end dates for the model simulation were 16 May and 15 June respectively. Model simulations were carried out for particles at depths of 0, 20 and 100 m but for the purpose of this report the 20 m simulation was selected as giving the closest approximation to the modal vertical distribution of mackerel eggs and larvae (Coombes *et al.*, 1996).

For purposes of quantifying the change in distribution between the start and end dates, the study area was divided into a number of strata (Fig. 2). The numbers of particles found in each strata at the beginning and end of the month were then calculated.

Distributions of First Winter Juveniles

Data were obtained from ICES winter (October-March) international coordinated bottom trawl surveys carried out on the continental shelf from the Bay of Biscay to the north west of Scotland. The survey series began in the winter of 1981/82. Trawl stations are at fixed positions within standard ICES ½ latitude x 1 longitude rectangles. Numbers in each haul are converted to numbers per hour and ascribed to age group using age length keys or in their absence using the assumption that all fish <24 cm are first winter fish and all larger fish are older. Assuming a mean spawning date of 1 June the juveniles caught during the survey period range in age from 4-10 months in age.

Data in each winter are first aggregated by quarter and the arithmetic mean number/h calculated per rectangle for that quarter. To calculate a single winter abundance index for each rectangle the arithmetic mean value of the two quarters is then taken. Winter abundance indices by subarea (Fig. 3) were then calculated by taking the arithmetic mean of the sampled rectangles within them. For each winter the relative abundance in each

subarea was then calculated by dividing the abundance index for the subarea into the sum of the indices from all areas.

Survival and Yearclass strength

Data on yearclass strength for the five years covered by the transport study were estimated by VPA and obtained from the 1995 mackerel assessment working group (Anon, 1996b).

The Model Description

The model

The Norwegian Ecological Model (NORWECOM) is a coupled physical, chemical, biological model system applied to study primary production and dispersion of particles eg fish larvae and pollution. The model system is fully described in Skogen (1993) (see also Aksnes *et al.* (1995) and Skogen *et al.* (1995)). In this study a coupled system with a circulation model and a transport model is used.

The circulation model

The circulation model is based on the wind and density driven Princeton Ocean Model (Blumberg and Mellor, 1980; Mellor, 1996). A 20 x 20 km horizontal grid covering the whole shelf area from Portugal to Norway, including the North Sea, has been used (Fig. 4). Vertically the model uses 12 sigma layers.

The forcing variables are six-hourly hindcast atmospheric pressure fields provided by the Norwegian Meteorological Institute (DNMI) (Eide *et al.*, 1985; Reistad and Iden, 1995) six-hourly wind stress (translated from the pressure fields by assuming neutral air-sea stability), four tidal constituents and fresh water runoff. To absorb inconsistencies between forced boundary conditions and model results, a seven gridcell "Flow Relaxation Scheme" (FRS) zone is used around the open boundaries (Martinsen and Engedahl, 1987). Due to a lack of data on surface heat fluxes, a "relaxation towards climatology" method is used (Cox and Bryan, 1984). During calm wind conditions, the surface temperature field will adjust to the climatological values after about 10 days (Oey and Chen, 1991). The net evaporation precipitation flux is set to zero.

North of a line passing through Brest (France) and south of Porcupine Bank, initial values for velocities, water elevation, temperature and salinity are taken from monthly climatologies (Martinsen *et al.*, 1992). South of this line initial values for salinity and temperature are taken from the Levitus dataset (Levitus, 1982), while velocities are computed using the thermal wind equation assuming zero net flux. Interpolations between monthly fields are used at the open boundaries. An exception to this rule is made in calculating velocities north west of the Iberian Peninsula (close to La Coruna). In this area data from continuous moorings in 1993/94 (Alonso *et al.*, 1995) are used, and assumed valid for all years.

Monthly data for fresh water runoff from the main rivers around the North Sea are taken from Baliño (1993), while data from French rivers were obtained from IFREMER. Total fresh water runoff from along the Norwegian and Swedish coast have also been estimated (Egenberg, 1993). In addition Spanish river discharge from one year (Lavin, pers. comm.)

is assumed valid for all years, and monthly means for fresh water runoff to the Irish Sea are taken from Anon (1990a).

The transport model

Interpolations between daily mean currents from the circulation model are fed into a Lagrangian particle tracking model to simulate the transport of fish larvae. The particles are released and fixed in certain depths. Particle diffusion is performed using a random walk procedure. No larval mortality is introduced into the model.

RESULTS

The Distribution of First Year Juveniles in Relation to the Distribution of Spawning

In Figure 5 the distribution of stage I mackerel eggs (Fig. 5a) is compared with the distribution of first year juveniles (Fig. 5b). Both figures are mean distributions derived from surveys over a number of years. In the case of the egg survey data, May/June distributions from the complete time series of the ICES triennial surveys have been used ie seven surveys over the period 1977-1995. In the case of the juvenile data a 14 year time series of distributions covering the winters from 1981/82 to 1994/95 has been used.

The distributions shown are confined to the area north of $43^{\circ}30'N$, where the time series of data is more extensive than further south. The distributions of both eggs and juveniles do however extend further south than this latitude. With regard to the northern limits of the underlying populations, stage I mackerel eggs have been found as far north as $60^{\circ}N$ (Anon, 1990b) but abundance in the area north of the standard survey area shown in Figure 4a is very low. With regard to juveniles their distribution may extend a little beyond the eastern boundaries shown in Figure 5b (north of Scotland and in the English channel) but results of winter bottom trawl surveys of the northern and southern North Sea do not indicate any significant quantities beyond the boundaries used. The western boundary of the egg distribution in Figure 5a should give a good indication of the western limits of spawning but in the case of the juvenile data the western boundary is defined by the shelf edge beyond which trawling was not undertaken. Very little is known about the distribution of juveniles offshore of the shelf edge, but it is generally assumed that they are scarce or absent in this area, with the possible exception of the area west of Ireland where the continental slope is much shallower than in other areas.

A comparison of the distributions in Figures 5a and b indicates some dispersal of the products of spawning to nursery grounds that overlap but are not coincident with the spawning grounds. Most notably a much higher proportion of juveniles are found in the north of the study area (eg north of $52^{\circ}30'N$) than is the case in the egg distribution, while in the latitudes of the Cornish peninsula and the Bay of Biscay the juveniles are much more inshore in their distribution than are the eggs.

Changes in Distribution of Mackerel Spawning

Figure 6a shows the change in the relative proportions of stage I mackerel eggs taken west of the shelf break in May/June in the seven triennial egg surveys carried out between 1977 and 1995. The area subdivisions used in the analysis are shown in Figure 1. The data

indicate a progressive increase in the proportion of spawning west of the shelf break (all areas combined) from 26% in 1980 to 81% in 1995, with the greatest shift between 1986 and 1989. With regard to individual areas Porcupine Bank and Celtic Sea show broadly similar trends to that of the total while in the Bay of Biscay there was very little variation between years except in 1980 when an unusually high proportion of spawning took place east of the shelf break as in all areas in that year.

Figure 6b shows the change in the relative proportions of spawning along the north/south axis of the sampling area using the same data set as above. The data indicate a relatively stable pattern between 1977 and 1986 with the Celtic Sea providing the major contribution to total egg production (57-72%), followed by Porcupine Bank (23-26%) and the Bay of Biscay (5-18%). Between 1986 and 1989 a marked northerly shift in distribution took place with egg production in the Porcupine Bank area increasing from 26-50% of total production accompanied by a comparable drop in the Celtic Sea and little change in the Bay of Biscay. From 1989 to 1995 the proportion of spawning in the Porcupine area remained relatively high, while in the Celtic Sea it fluctuated but always remained well below the levels of the previous four surveys. In 1995 the proportion of spawning in the Celtic Sea fell to its lowest level with increased proportions both to north and south.

Figures 7a-e show the distributions of stage I mackerel eggs in the month of May in the five surveys between 1980 and 1992, these data were used in the dispersal study described later.

Changes in Distribution of First Winter Juveniles

Figure 8 shows the change in relative proportions of juveniles taken in different areas of the study area (Fig. 3) over a 14 winter time series (1981/82-1993/94). The data indicate a fluctuating trend to a more northerly distribution pattern in recent years with the most marked change occurring between the winters of 1988/89 and 1989/90. The proportion of annual abundance taken in the three most northerly areas ie north of 52°30'N remained low from 1981-1988 at a mean value of around 10% while in the following six winters it increased to around 56%.

Circulation Within the Study Area

Figure 9 shows a schematic view of the generally accepted circulation in the study area based on work by Booth and Ellett (1983), Ellett *et al.* (1986) and Pingree and Le Cann (1990). This figure shows the location and continuity of the poleward flowing slope current and demonstrates its central position in relation to the mackerel spawning grounds (Figs 7a-e). Assuming this flow pattern, its potential as an important parameter in determining transport to the nursery areas is clear. In reality, however, it is recognised that this continuity is subject to both seasonal and regional fluctuations with the flow being weaker in summer than in winter and with reversals of direction more common in the south and centre of the area than in the north. Figure 10 demonstrates how the actual flow pattern can vary from this paradigm. It shows the modelled mean circulation at 20 m during the month of May - the month selected for the transport study - for the years 1976-1994 inclusive. Unlike Figure 9 the modelled data imply an almost continuous southerly flow along the slope west of the 200 m contour in the mackerel spawning area. The data indicate this to be the strongest area of transport in the study area extending for some 20-50 nmiles west of the shelf break - an important area for mackerel spawning. Circulation on the shelf itself is generally weak and non directional with notable exceptions off north west Ireland where there is a north easterly flow shoreward from the shelf break and in the Bay of Biscay

where there is shoreward flow across the shelf break, both of potential importance to mackerel larval transport. The model also indicates weak shoreward transport in the area east of Porcupine - another potentially important area for mackerel larval transport. Other features of the model such as the strong transport some 4° west of the shelf break between 50° and 58°N are too far west to be of any likely significance to mackerel larval dispersal.

Transport of Eggs and Larvae

1. Modelled particle transport at 20 m depth along four transects in the 1980-1992 surveys

Spaghetti plots of modelled particle transport in the five egg survey years between 1980 and 1992 are given in Figures 11a-e. The plots represent one months transport between 16 May and 15 June. The salient feature of these plots is their similarity between years. In all years and along all four transects the area of greatest transport lay on the western side of the shelf break with the direction of transport in this zone almost uniformly towards the south or south east. Only at a couple of stations along transect 2 was there some evidence of a northerly component to the transport. On these stations transport was towards the north east and it is interesting to note that this occurred in four out of the five survey years on one station and was most marked in 1992. Another important feature of the model-data is that it indicates the shelf-break to be a convergence zone.

With regard to transport on the shelf, the spaghetti plots indicate much lower values here and with more variable direction than west of the shelf break. The most marked difference to other years was in 1992 when there was a northerly component to transport on the shelf especially from the two most northerly transects.

2. Modelled transport of egg production in the 1980-1992 surveys

Table 1 shows the number of eggs in each of the sub areas shown in Figure 2 before and after 31 days modelled transport, starting on 16 May in each of the five survey years between 1980 and 1992. For purposes of interpretation, these data are combined into larger area groupings to show north/south transport (Fig. 12) and east/west transport (Fig. 13).

The salient feature of the data shown in Figure 12 is the broad similarity in transport pattern between years. For example taking the central area (subareas 4a-d combined), which is the area of highest egg production, there is a decrease in abundance in all years indicating net transport out of this area. The majority of this transport is towards the south where abundance in northern Biscay (subareas 5a,b) is seen to increase markedly in four out of the five years modelled (the exception being 1989). The same very marked increase in abundance is also evident in southern Biscay (subareas 6a,b) in the 1983, 1986 and 1989 surveys and in the area south of Biscay indicating an immigration of particles into all these areas from the north. In the two most northerly areas there also appears to be a typical pattern with 1989 the exception. Thus, west of Ireland a small decrease in abundance occurred in four out of five years while further north, to the west of Scotland, a small increase occurred in two out of three years sampled. In typical years therefore the data indicate net transport out of the area west of Ireland towards both north and south and net transport into western Scotland from the south. 1989 differed from other years in that there was a marked increase in abundance west of Ireland from start to end of the transport period and decreases west of Scotland and in northern Biscay. These data indicate that in 1989 there was transport of spawning products into west of Ireland from both north and

south while in northern Biscay emigration of spawning products towards the south occurred as normally but immigration from the north was much reduced compared to the other years resulting in an atypical decline in abundance in the area.

In Figure 13 the data from Table 1 are combined into inshore and offshore area groupings roughly equivalent to east and west of the shelf break. The results indicate that in all years except 1992 there was a net increase in abundance offshore of the shelf break at the expense of abundance inshore over the 31 days of transport. In all years this increase was mainly accounted for by transport from the north into the offshore area of Biscay.

Yearclass Strength and Distribution

The abundances of first winter fish as estimated by VPA (Anon, 1996b) are compared with indices of westerly and northerly distribution of eggs in Table 2.

The data in Table 2 provide no convincing correlations between distribution and survival. Thus, although the strongest yearclass, 1980, also has the most onshelf distribution, the second strongest yearclass, 1989, has the second most westerly distribution.

DISCUSSION

A comparison of the combined annual distributions of eggs and first year juveniles (Figs 5a,b) indicates that, although fairly similar, these are not coincident. In particular the distribution of juveniles extends further north than that of the eggs while in the latitudes of Cornwall and in the Bay of Biscay the distribution contains a strong inshore element which is absent from the egg distributions. Distribution of juveniles west of the shelf break remains an unknown factor but in the absence of any evidence of their presence in this area our supposition is that, with the possible exception of the Porcupine Bank area, they are probably scarce or absent much beyond the shelf break, in contrast to the eggs. It is clear from the differences between spawning and nursery areas that some transport mechanism (active or passive) must operate to move individuals from the spawning grounds to the nursery grounds.

By comparing Figures 5a and b to modelled circulation during the spawning season (Fig. 10) some interesting insights into the possible influence of circulation on juvenile distributions may be drawn. One of the salient features of the modelled circulation is the lack of transport from offshelf waters onto the shelf in the central latitudes (48°N to 51°N) of the spawning area. This is one of the areas of highest egg production, so the fate of these eggs is likely to be very important for the prospects of the stock. In the absence of a passive transport mechanism to carry these onto the shelf and hence to the nursery grounds two possibilities arise. One is that the products of spawning are retained in this area, can find sufficient food to grow and then settle there, and later, actively migrate into the Celtic Sea. The other is that the spawning products are retained in the area, cannot find sufficient food and are lost to the population. To the north and south of these latitudes, however, there is some evidence of onshelf transport. For example, between 51°N and 54°N - an important spawning area in recent years - there is weak transport towards and across the shelf break east of Porcupine Bank, while north of 54°N there is relatively strong transport from the shelf break towards the north east. The shelf area north of 51°N has become a particularly important nursery area in recent years (winter 1989/90 onwards) and the high abundance and particular distribution of juveniles between 55°N and $56^{\circ}30'\text{N}$ (Fig. 5b) correspond

quite closely with the modelled circulation pattern in this area. This indicates that passive transport could provide a likely route by which eggs spawned in the north of the spawning area reach northern nursery areas. Similarly south of 48°N in the Biscay area there is also evidence of on-shelf and in-shore transport which could contribute to the more inshore distribution of juveniles in this area.

Juveniles are also abundant at the shelf break along much of their geographical range and this corresponds to a convergence zone as demonstrated by the spaghetti plots. By contrast the modelled circulation data provide no evidence of any route by which passive transport could account for the high abundance of juveniles in the inshore waters around Cornwall.

The egg distribution data shown in Figures 6a and b and the juvenile distribution data in Figure 8 demonstrate that a marked north westerly shift in spawning occurred between 1986 and 1989 surveys while a marked northerly shift in the distribution of first winter juveniles took place between the winter surveys of 1988/89 and 1989/90. The coincidence in timing of these changes suggested a possible common cause, with a change to a more northerly circulation pattern - leading to increased larval transport to the north - as a likely candidate. The modelled transport pattern shown in Figures 11a-e and 12, provide very little evidence to support this hypothesis. Contrary to expectation, the spaghetti plots and the modelled transport of spawned particles indicated that, in all five years investigated transport over most of the important slope area was predominantly to the south and not to the north. Furthermore, the data were characterised by a high degree of similarity between years and did not point to any very marked differences which might account for the much more northerly distribution of juveniles from 1989/90 onwards. There were however some subtle differences between years which merit comment. Thus 1989 - the year in which the biggest change in spawning and juvenile distributions occurred - was the most different from the other modelled years. In this year the transport data (Fig. 12) indicated a marked increase in abundance of particles in the west of Ireland area originating from further south, while in all other egg survey years there was net transport out of this area towards the south. Furthermore when the transport data for western Ireland in this figure are compared with the proportion of juveniles north of 52°30'N in the same years (Table 3) the ranking order of the two data sets are the same ie when net transport of particles from the area is low or even negative the proportion of juveniles in the north is highest while when transport south is highest the proportion of juveniles in the north is lowest.

The analysis carried out in this investigation indicates that, contrary to expectation, transport over most of the slope area where mackerel spawning occurs during the peak spawning season, is towards the south. This appears to be a relatively constant feature in all years. On this basis alone the expectation would be that if passive transport in the first month after spawning was the main determinant of juvenile distribution then most juveniles would be found in central and southern areas of the distributional area and numbers in the north much scarcer than is indicated by the trawl survey data. The conclusion must therefore be that changes in circulation alone are not the main contributor to a change in the distribution of juveniles.

It seems likely that the change in distribution of both spawning and nursery grounds at the same time is non coincidental and has a common oceanographic basis although this remains as yet unknown. Although the circulation and transport data do not explain either the magnitude of the northerly shift in nursery grounds or the exact locations of some of these, they nonetheless appear to have some influence on them. Thus, it is evident that when there is a northward shift in spawning there is a circulation route by which the northern

component of eggs can be transported passively to nursery grounds further north. A mechanism also appears to exist by which offshelf spawned eggs can be transported across the shelfbreak towards observed nursery areas in Biscay.

On the other hand the distribution of juveniles in the important nursery grounds around Cornwall would seem to indicate active migration to this area.

The remaining unexplained discrepancy between the high abundance of juveniles in the north in recent years compared to more southerly spawning grounds (over which transport is predominantly towards the south) suggests that there may also be significant differences in survival rate between the north and south with higher survival in the north.

Investigations of yearclass strength in relation to the distribution of spawning did not support the hypothesis that strong yearclasses are associated with on-shelf spawning.

CONCLUSIONS

The general conclusions of this study on the observed changes in the distribution of juveniles are:

1. They are not caused by any major change to a more northerly circulation pattern.
2. The northward shift in the spawning grounds and the circulation pattern demonstrated by the transport model provide a mechanism which goes some way towards explaining the northward shift in nursery area.
3. Both passive transport in the first month of life and active migration thereafter contribute to the observed distribution of nursery grounds.
4. Survival of spawning products may be higher in the northern parts of the spawning area than in the south.
5. Good yearclasses are not necessarily associated with on-shelf spawning.

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REFERENCES

- Aksnes, D.L., Ulvestad, K.B., Baliño, B., Berntsen, J., Egge, J. and Svendsen, E. 1995. Ecological modelling in coastal waters: towards predictive physical-chemical-biological simulation models. *Ophelia*, 41, 5-36.

- Alonso, J., de Castillejo, F.F., Diaz del Rio, G., Marcote, M. and Casas, G. 1995. Preliminary results of current measurements in the north west of the Iberian Peninsula. Tech. Rep. MORENA Sci. and Tech. Rep. No. 1. Centro Oceanografico de La Coruña.
- Anon. 1990a. Hydrological Data UK - 1990 Year Book. Institute of Hydrology, Wallingford, Oxon, UK. ISBN 0 948 540 36 2.
- Anon. 1990b. Report of the mackerel/ horse mackerel egg production working group. ICES CM 1990/H:2 89pp (mimeo).
- Anon. 1996a. Report of the mackerel/horse mackerel egg production working group. ICES CM 1996.
- Anon. 1996b. Report of the working group on the assessment of mackerel, horse mackerel, sardine and anchovy. ICES CM 1996/Assess:7.
- Baliño, B.M. 1993. Nutrient inputs to the North Sea, Skagerrak and Kattegat. River concentrations and loads from 1980 to 1990. Tech. Rep. HOV-senteret, Høyteknologisenteret, Bergen, Norway.
- Blumberg, A.F. and Mellor, G.L. 1980. A coastal ocean model. In: *Mathematical Modelling of Estuarine Physics*, Sunderman, J. and Holtz, K.P. (eds). Springer-Verlag, Berlin, pp203-214.
- Booth, D.A. and Ellett, D.J. 1983. The Scottish continental slope current. *Cont. Shelf Res.* 2, 127-146.
- Coombs, S.H., Morgans, D. and Halliday, N.C. 1996. The vertical distribution of eggs and larvae of mackerel (*Scomber scombrus*). ICES CM 1996/S:47.
- Cox, M.D. and Bryan, K. 1984. A numerical model of the ventilated thermocline. *J. Physical Oceanography*, 14, 674-687.
- Egenberg, B. 1993. The relationship between hydrographical variability in coastal water and meteorological and hydrological parameters. M.Phil. thesis, Geophysical Institute, University of Bergen, Norway. In Norwegian.
- Eide, L.I., Reistad, M. and Guddal, J. 1985. Database av beregnede vind og bølgeparametre for Nordsjøen, Norskehavet og Barentshavet. *DNMI report*.
- Ellett, D.J., Edwards, A. and Bowers, R. 1986. The hydrography of the Rockall Channel: an overview. *Proc. Roy. Soc. Edin. B*, 88B, 61-83.
- Levitus, S. 1982. Climatological atlas of the world ocean. *NOAA Prof. Pap.*, 13, 173pp.
- Lockwood, S.J., Nichols, J.H. and Dawson, W.A. 1981. The estimation of a mackerel (*Scomber scombrus* L.) spawning stock size by plankton survey. *J. Plank. Res.*, 3, 217-233.

- Martinsen, E.A. and Engedahl, H. 1987. Implementation and testing of a lateral boundary scheme as an open boundary condition in a barotropic ocean model. *Coastal Engineering*, **11**, 603-627.
- Martinsen, E.A., Engedahl, H., Ottersen, G., Adlandsvik, B., Loeng, H. and Baliño, B. 1992. MetOcean MOdeling Project, Climatological and hydrographical data for hindcast of ocean currents. Tech. rep. 100. The Norwegian Meteorological Institute.
- Mellor, G.L. 1996. User's guide for a 3-dimensional, primitive equation, numerical ocean model.
- Pingree, R.D. and Le Cann, B. 1990. Structure, strength and seasonality of the slope currents in the Bay of Biscay region. *J. Mar. Biol. Ass. UK*, **70**, 857-885.
- Oey, L.-Y. and Chen, P. 1991. A Model Simulation of circulation in the north-east Atlantic shelves and seas. Contribution No 6 of the Stevens Institute of Technology Ocean Modelling group.
- Reistad, M. and Iden, K.A. 1995. Updating, correction and evaluation of a hindcast data base of air pressure, winds and waves for the North Sea, Norwegian Sea and the Barents Sea. Tech. Rep. 9. Det Norske Meteorologiske Institutt.
- Skogen, M.D. 1993. A User's guide to NORWECOM, the NORWegian ECOlogical Model system. Tech. Rep. 6. Institute of Marine Research, Division of Marine Environment, Pb.1870, N-5024 Bergen.
- Skogen, M.D., Svendsen, E., Berntsen, J., Aksnes, D. and Ulvestad, K.B. 1995. Modelling the primary production in the North Sea using a coupled 3 dimensional physical chemical biological ocean model. *Estuarine, Coastal and Shelf Science*, **41**, 545-565.

TABLE 1

Distribution of spawning particles before and after 31 days transport

Area	1980		1983		1986		1989		1992	
	Before	After	Before	After	Before	After	Before	After	Before	After
1a									0	3
1b					53	56	62	0	2	0
2a			0	2	15	0	5	70	0	22
2b					304	456	489	167	41	31
3a			713	275	320	77	178	926	1036	736
3b	300	113	226	353	333	358	129	823	30	260
4a	3	35	430	649	902	174	2600	1756	2756	1495
4b	1731	1643	6169	3362	4533	3359	2931	2564	1987	2403
4c	300	230	459	913	782	528	926	650	186	116
4d	0	6	0	26	2	0	0	28		
5a	33	333	505	1475	824	1942	1773	1465	0	880
5b	222	191	204	227	123	113	822	600	8	97
6a	0	143	87	1330	8	1247	10	1020	37	37
6b	342	149	69	190	20	0	228	85	109	68
South	0	84	0	35					0	22

Key to areas

1a	VIa,b	West Scotland	NW
1b	VIa	West Scotland	NE
2a	VIa,b	West Scotland	SW
2b	VIa	West Scotland	SE
3a	VIIIb	West Ireland	W
3b	VIIc	West Ireland	E
4a	VIIIk	SW Ireland	W
4b	VIIj	SW Ireland	E
4c	VIIgh	Celtic Sea	
4d	VIIef	Cornwall	
5a	VIIIa	Biscay	NW
5b	VIIIa	Biscay	NE
6a	VIIIb	Biscay	SW
6b	VIIIb	Biscay	SE

TABLE 2

Comparison of yearclass strength and indices of westerly and northerly distribution

Year class	Abundance ¹		Westerly Index ²		Northerly Index ³	
	No	Rank	%	Rank	%	Rank
1980	5,624	1	26	5	23	5
1983	1,293	5	44	4	24	4
1986	3,301	3	49	3	26	3
1989	4,480	2	75	2	50	1
1992	2,600	4	81	1	40	2

¹Estimated number of one year old recruits x 10⁻⁶ from VPA (Anon, 1996a)²Percentage of total egg abundance west of shelf break (for area split see Fig. 1)³Percentage of total eggs in Porcupine area (see Fig. 1)

TABLE 3

A comparison between particle transport west of Ireland (52°30'N-54°30'N) and the proportion of western juvenile abundance north of 52°30'N

Year	Transport		Juvenile abundance	
	Index ¹	Rank	%	Rank
1980	0.38	5	No data	No data
1983	0.67	3=	0	4
1986	0.67	3=	3.5	3
1989	5.70	1	57.0	1
1992	0.93	2	43.0	2

¹index = nos particles after 31 days transport / nos particles at start

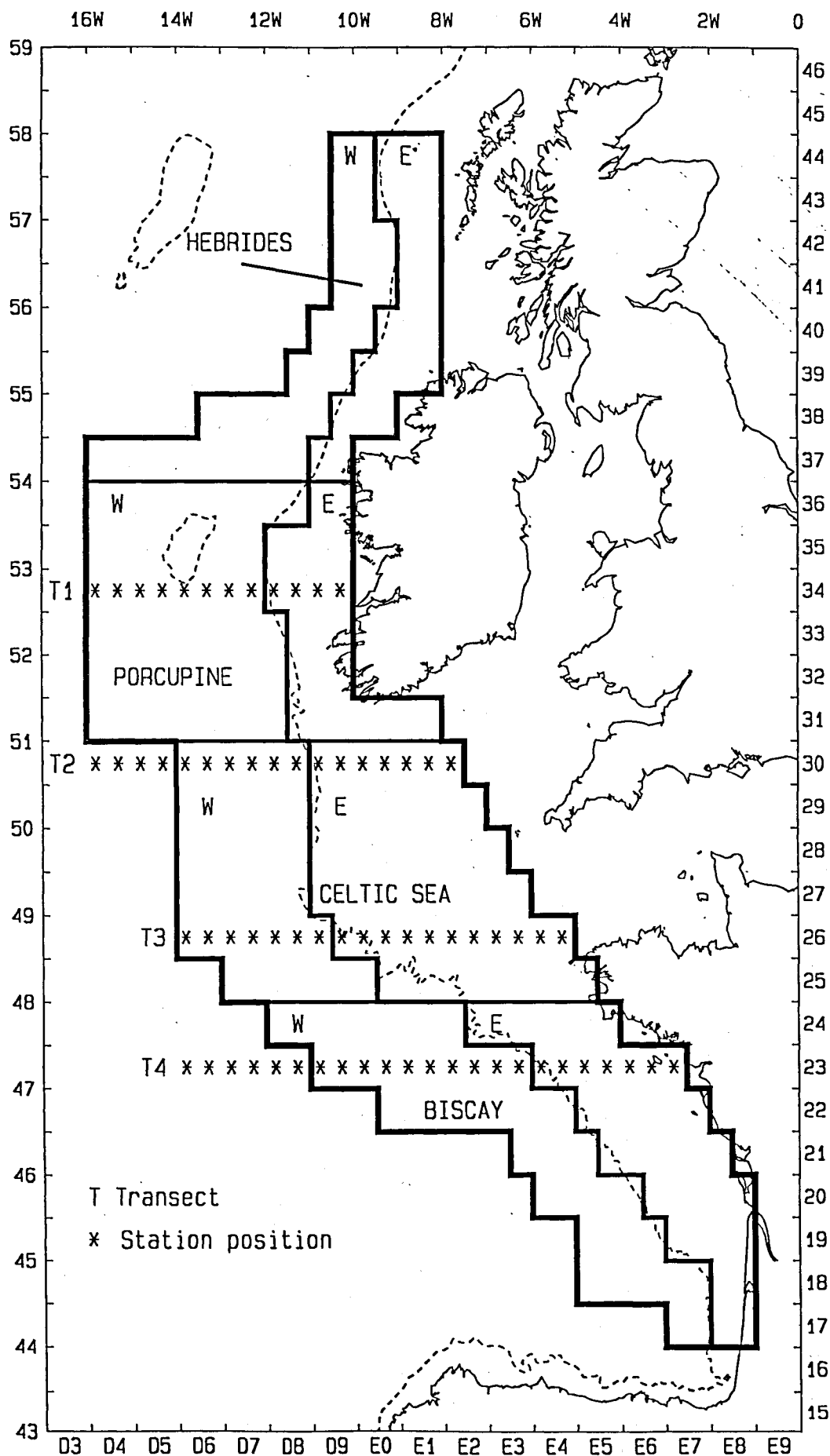


Figure 1 Subareas used to investigate changes in mackerel egg distribution and transects used in egg transport studies.

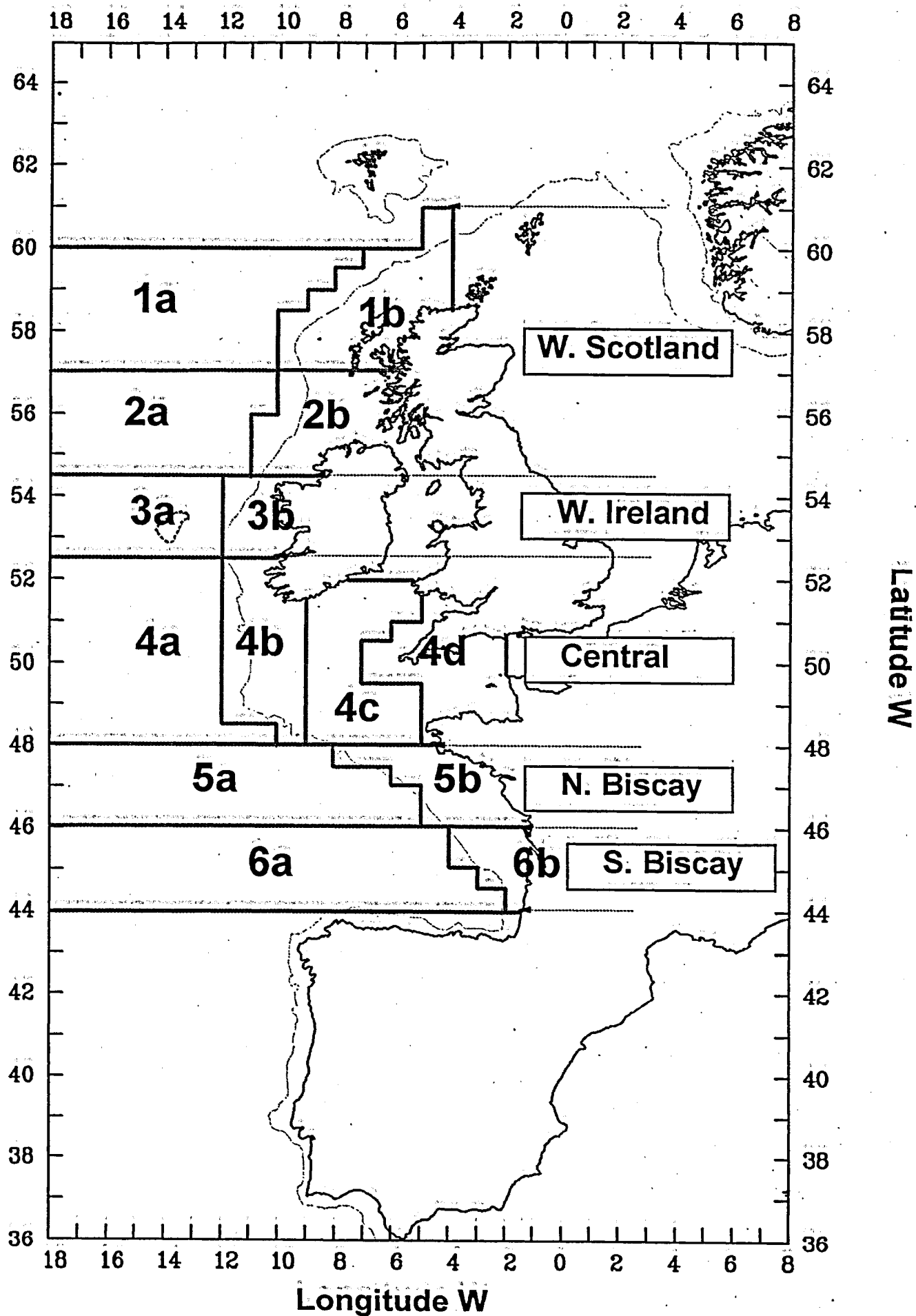


Figure 2 Areas used to study transport of spawning particles over 31 day period (16 May - 15 June).

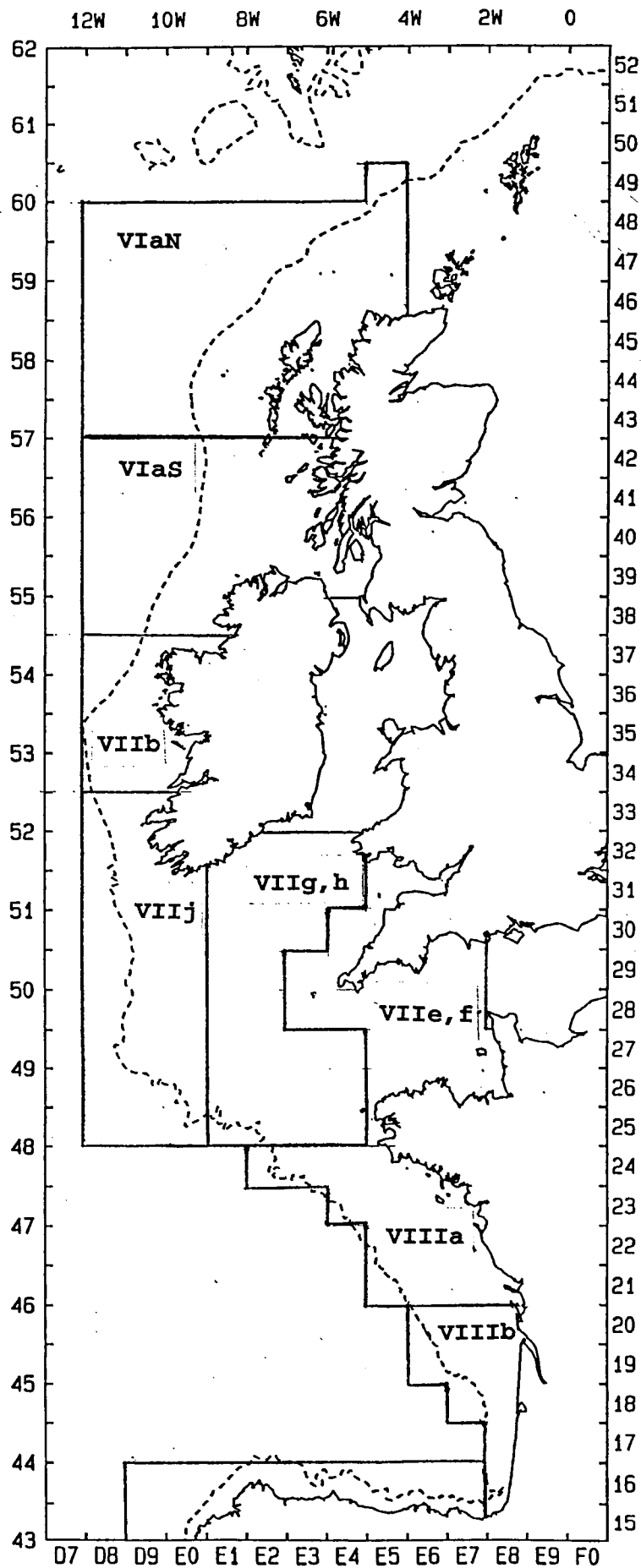


Figure 3 - Areas used in juvenile distribution study.

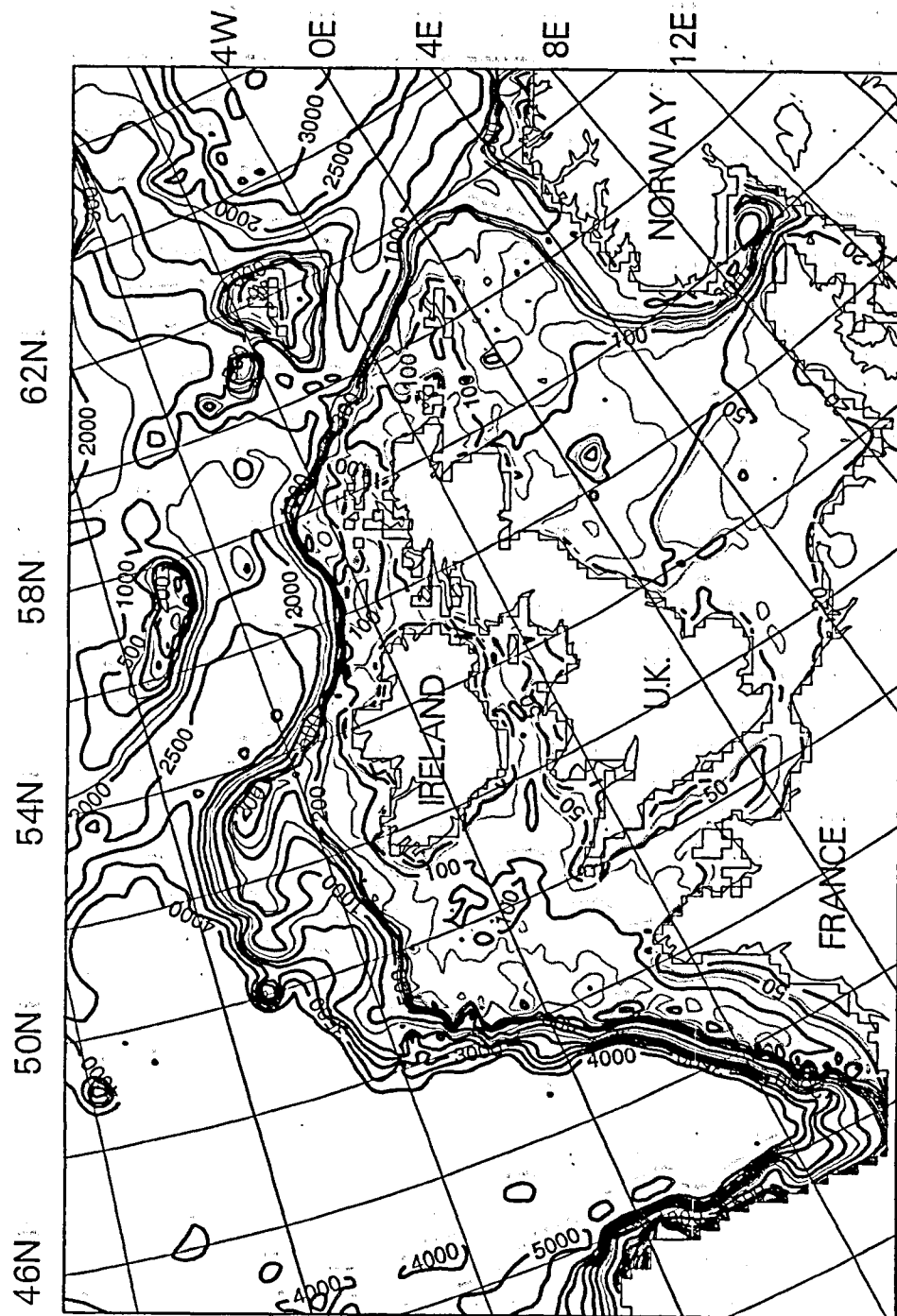


Figure 4 Area used for circulation model showing bottom topography.

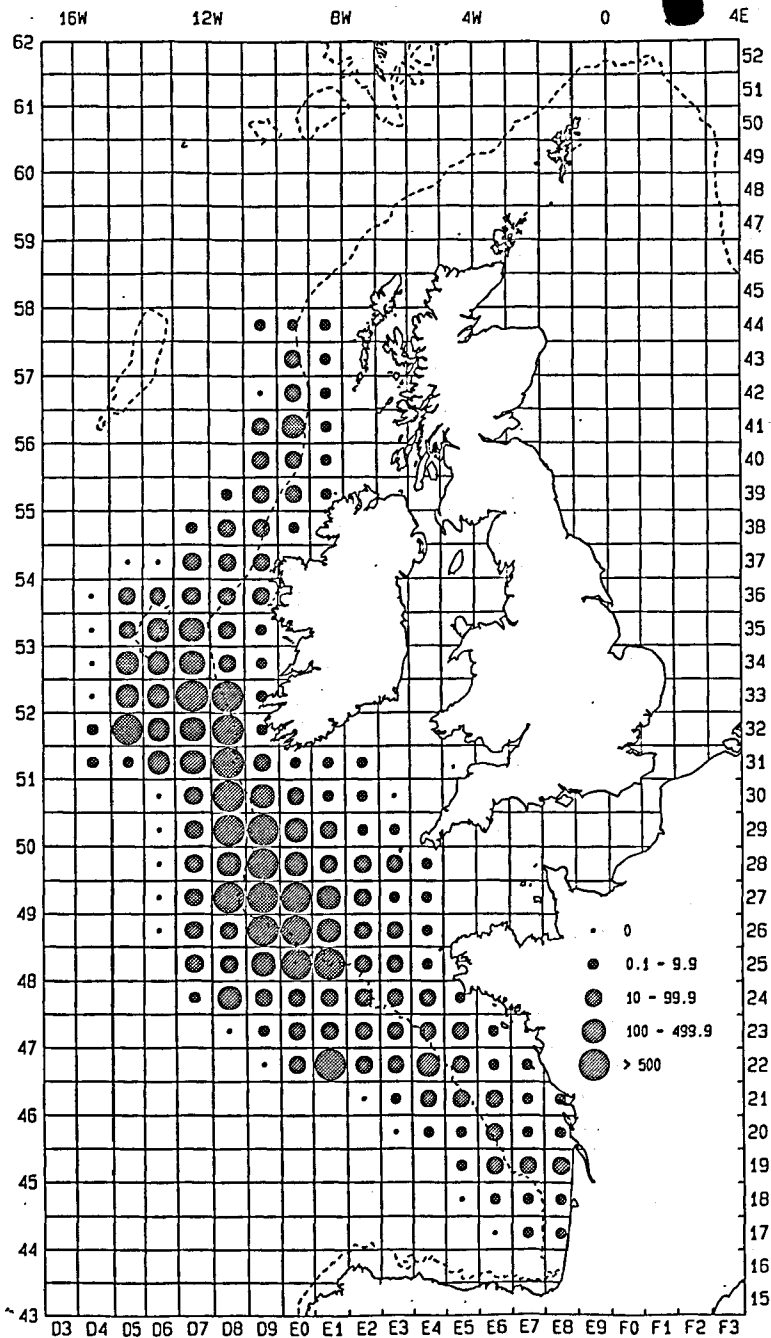


Figure 5a Mean number of mackerel eggs/m²/day 1977-1995.

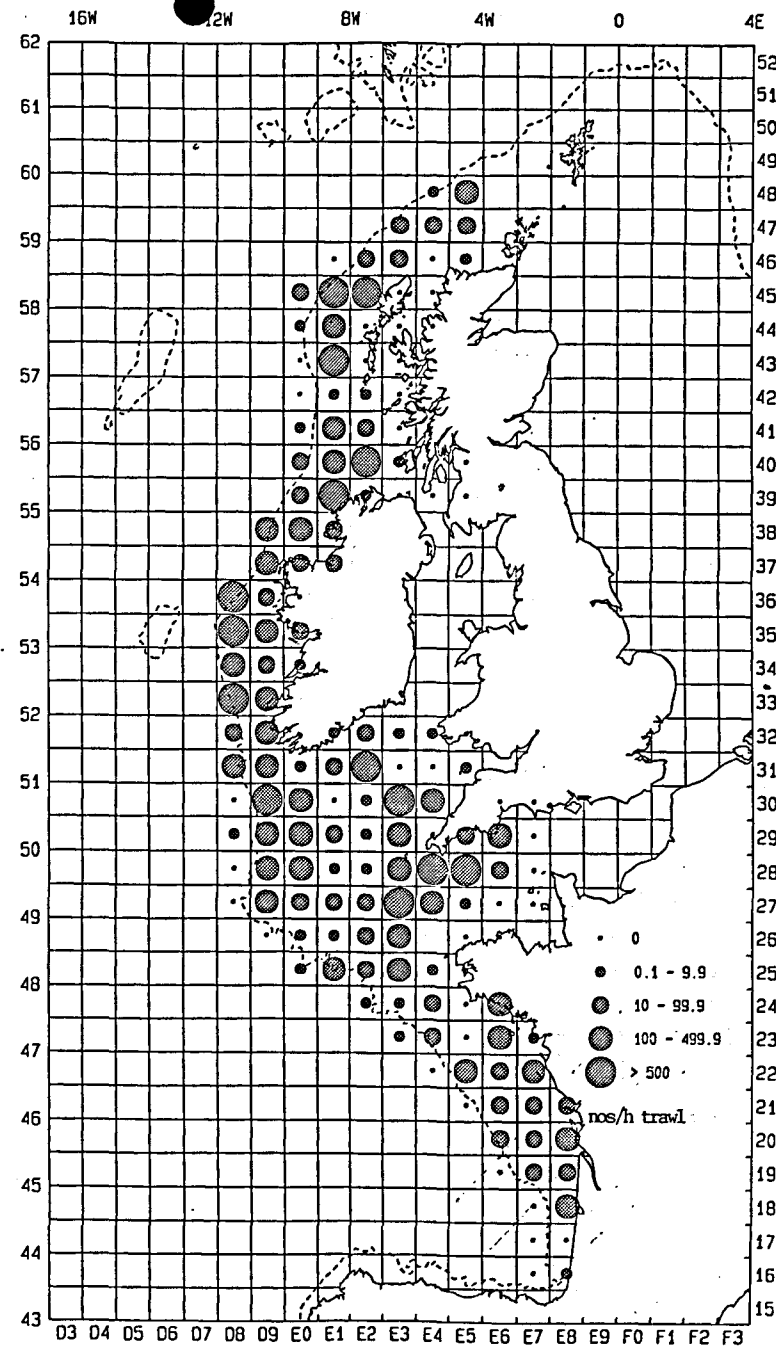


Figure 5b First winter mackerel distribution 1981/2-1994/5.

PERCENTAGE
OF
SPAWNING
WEST
OF THE
SHELF BREAK

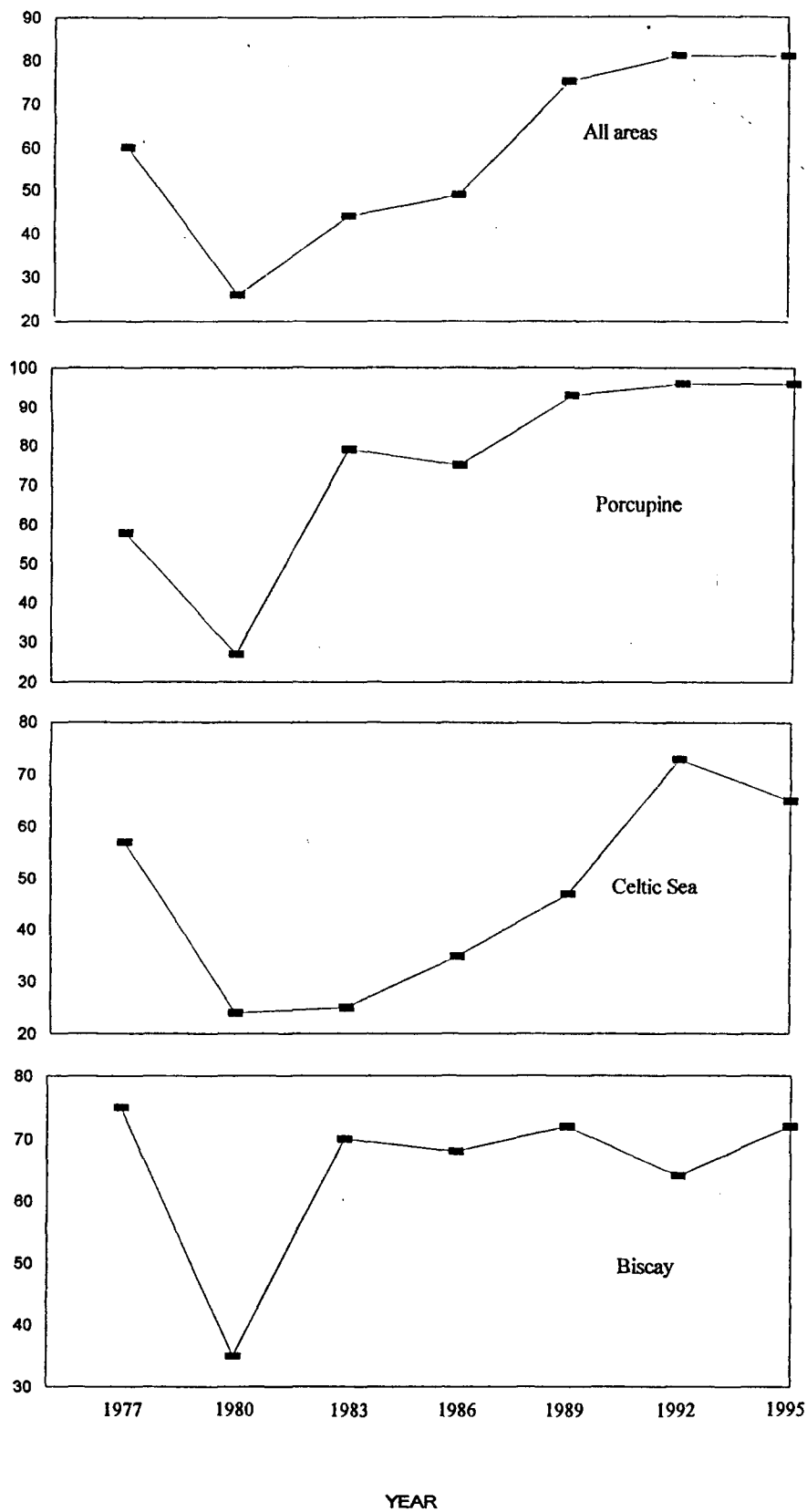


Figure 6a Changes in the proportion of mackerel spawning west of the shelf break.

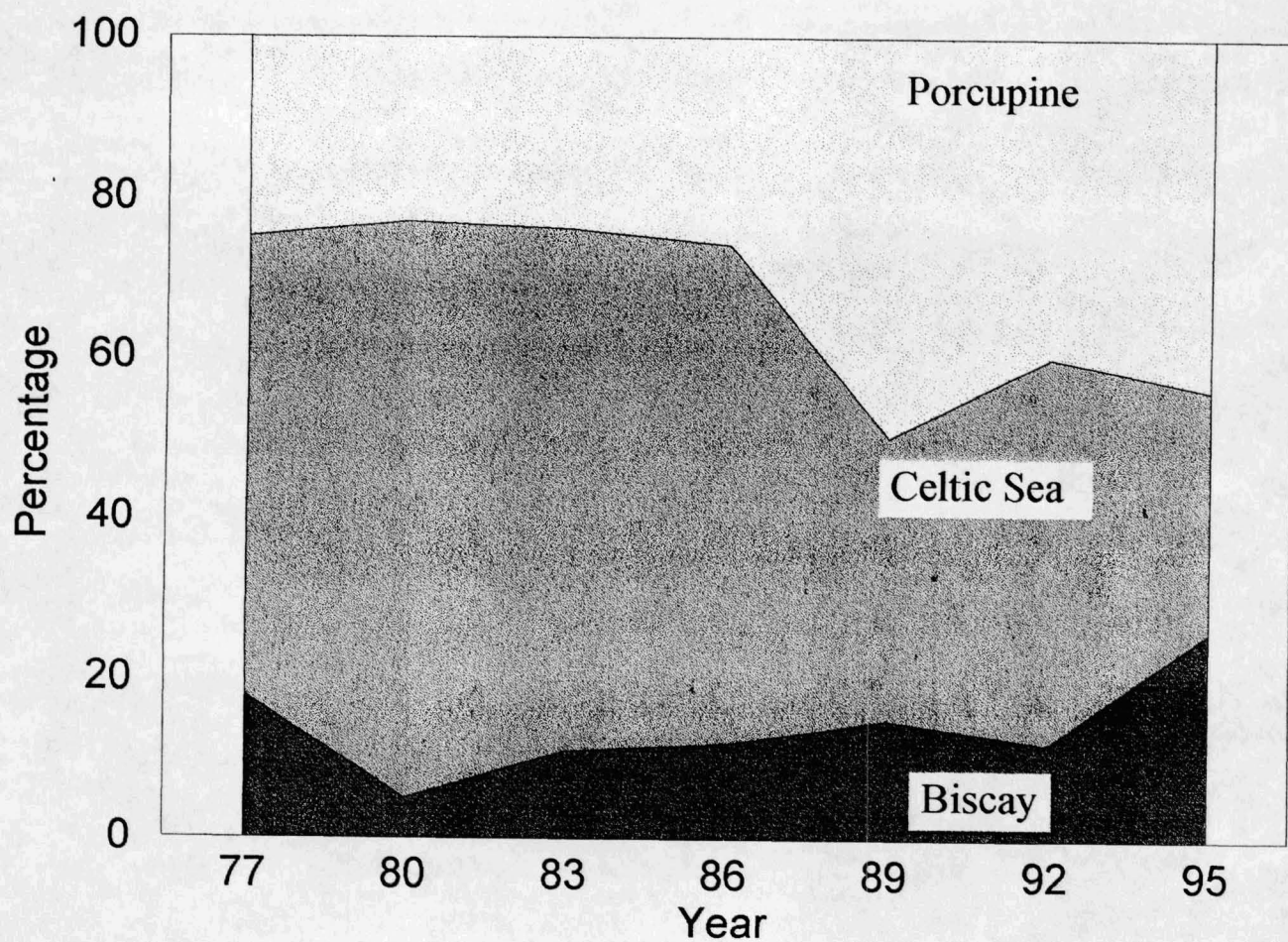


Figure 6b Changes in proportion of mackerel spawning along north-south axis of sampling area.

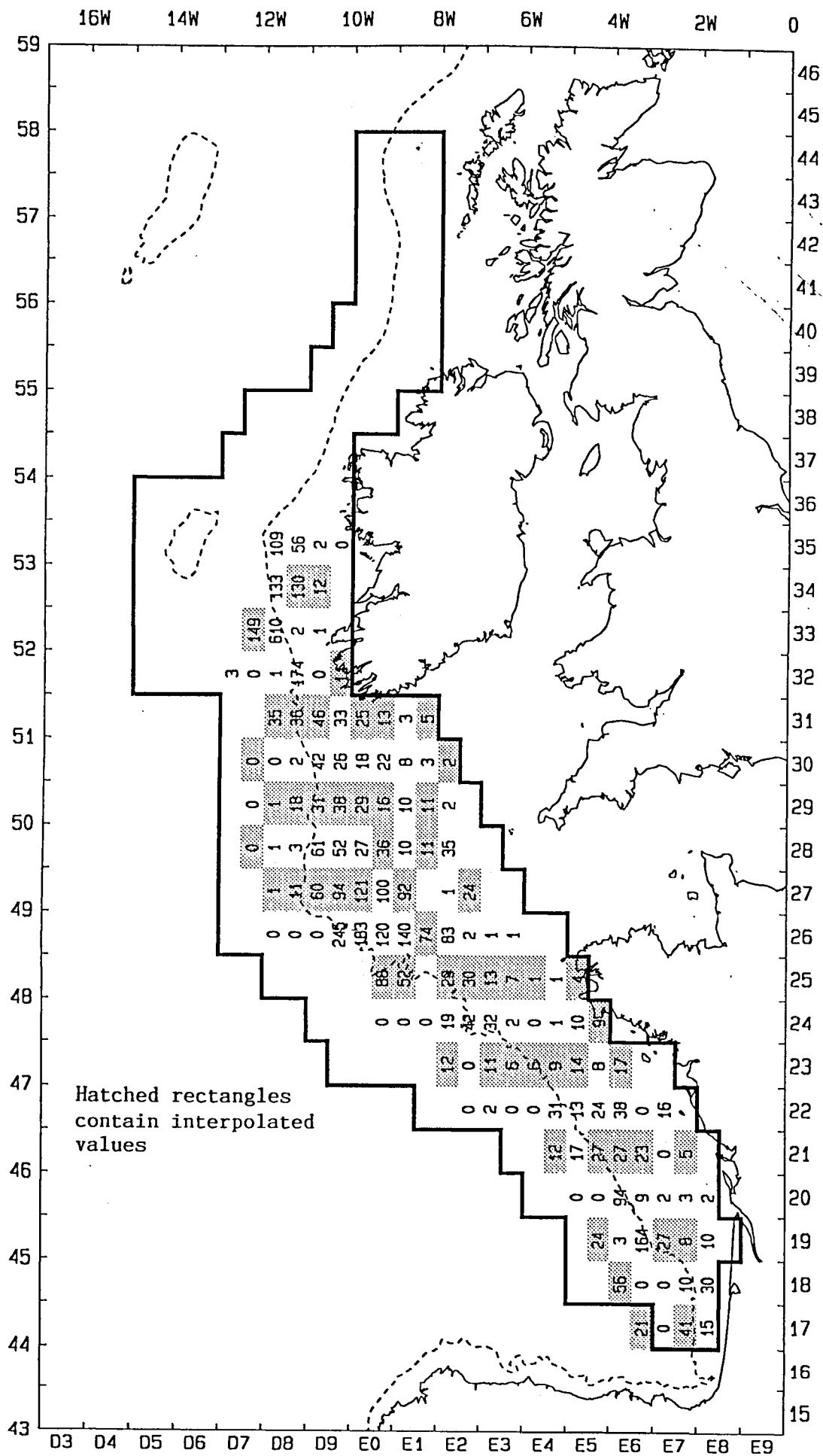


Figure 7a Mackerel nos/m²/day by rectangle from 1-31 May 1980.

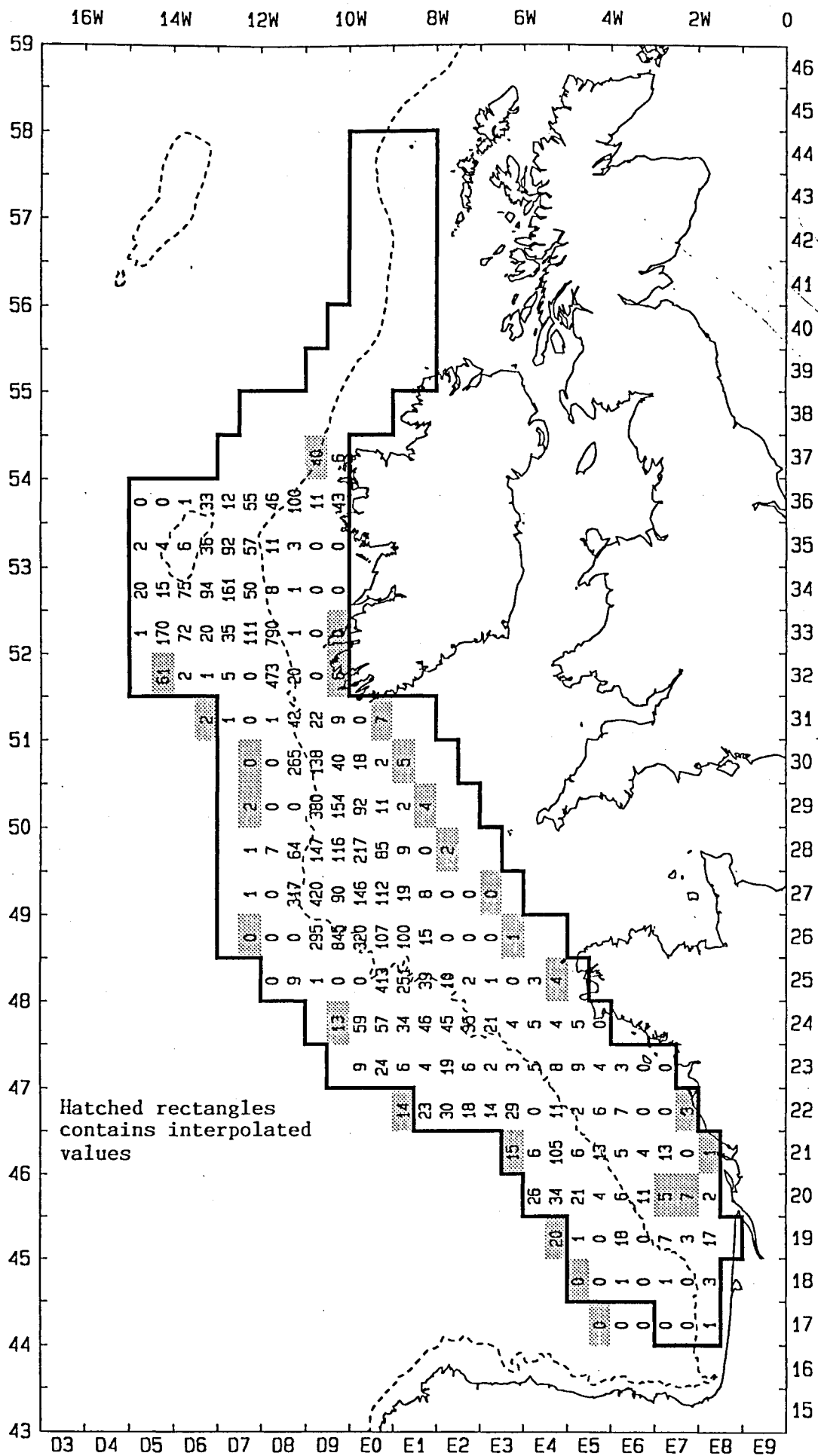


Figure 7b Mackerel nos/m²/day by rectangle from 1-31 May 1983.

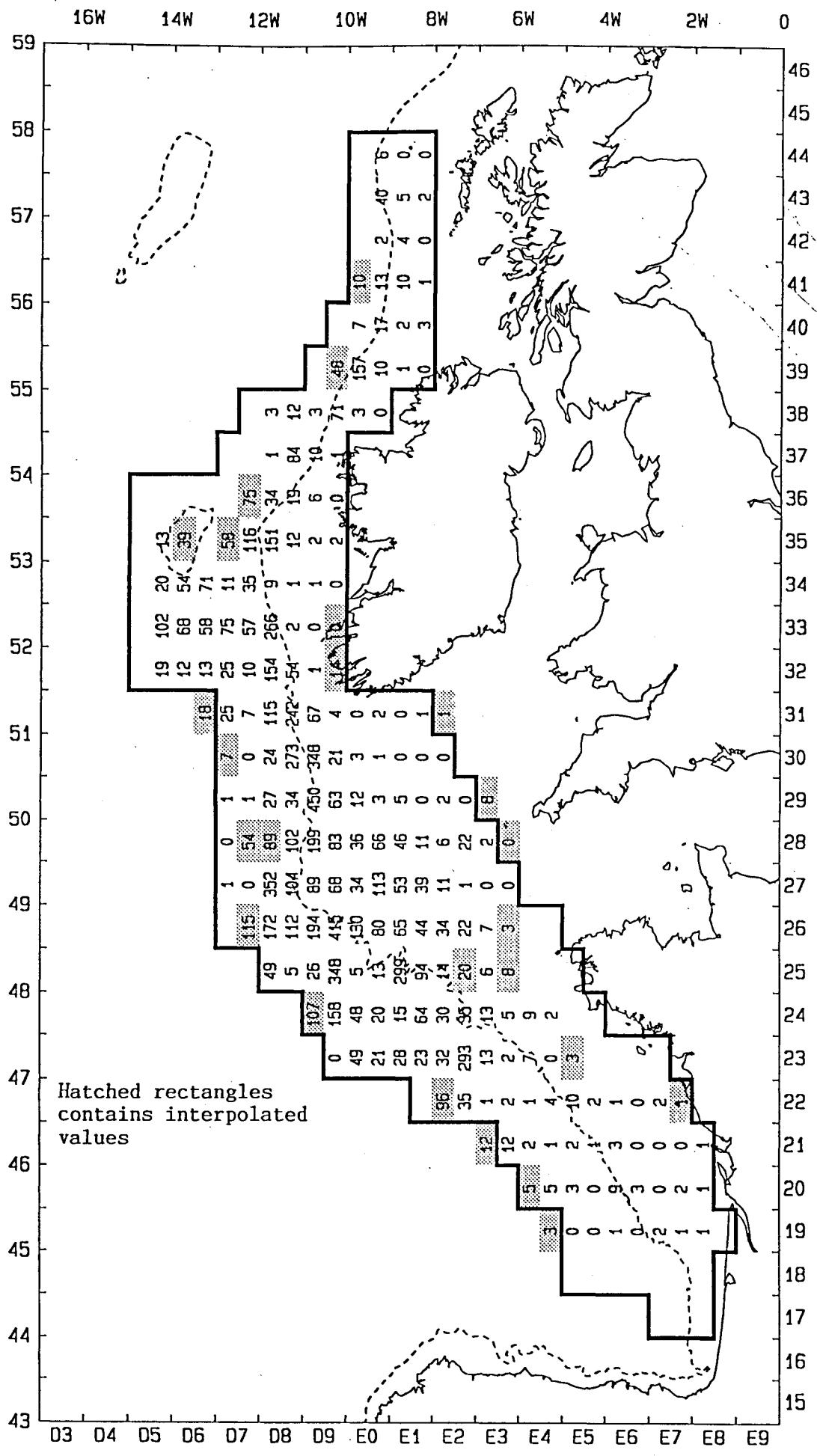


Figure 7c Mackerel nos/m²/day by rectangle from 1-31 May 1986.

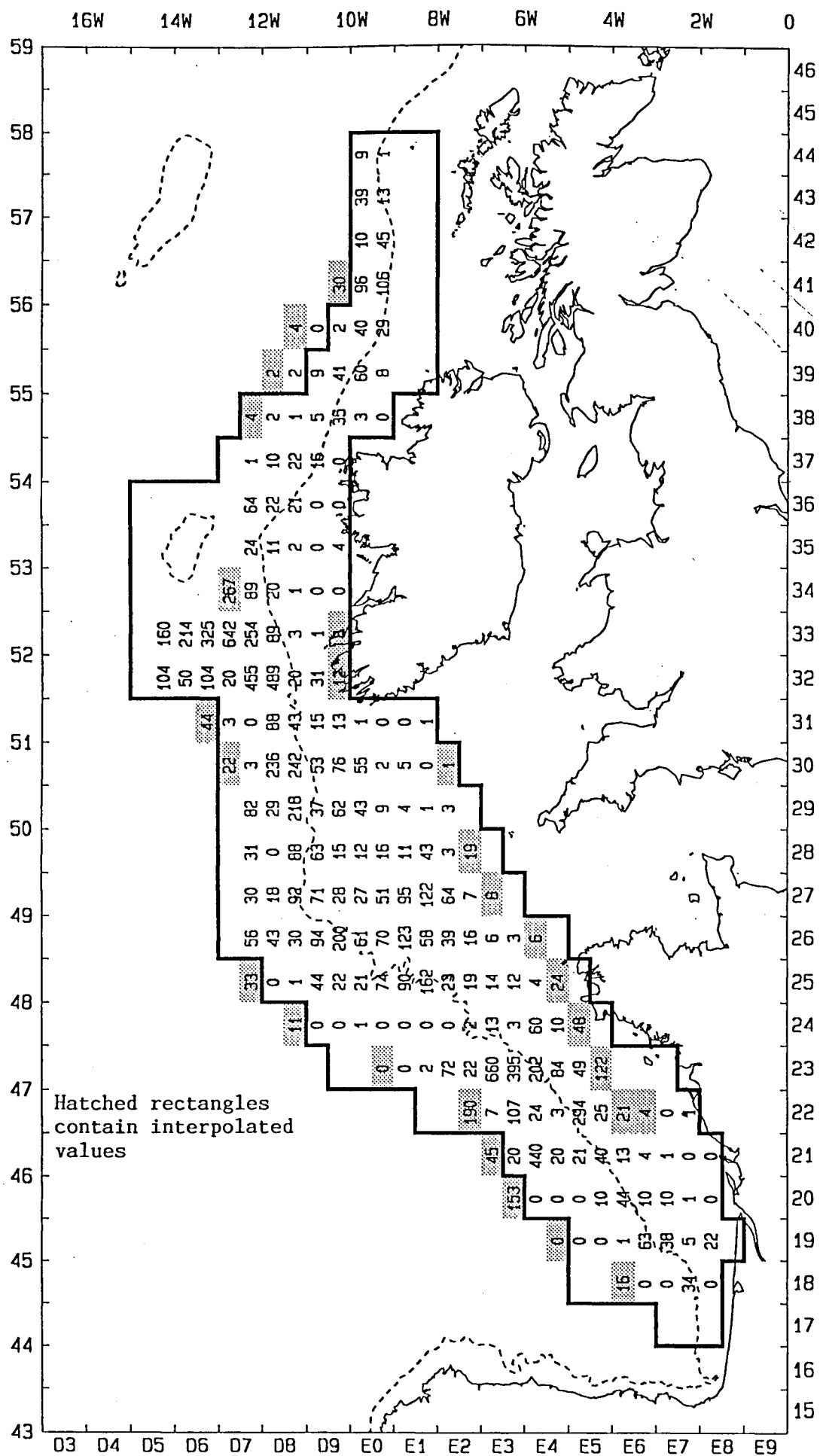


Figure 7d Mackerel nos/m²/day by rectangle from 1-31 May 1989.

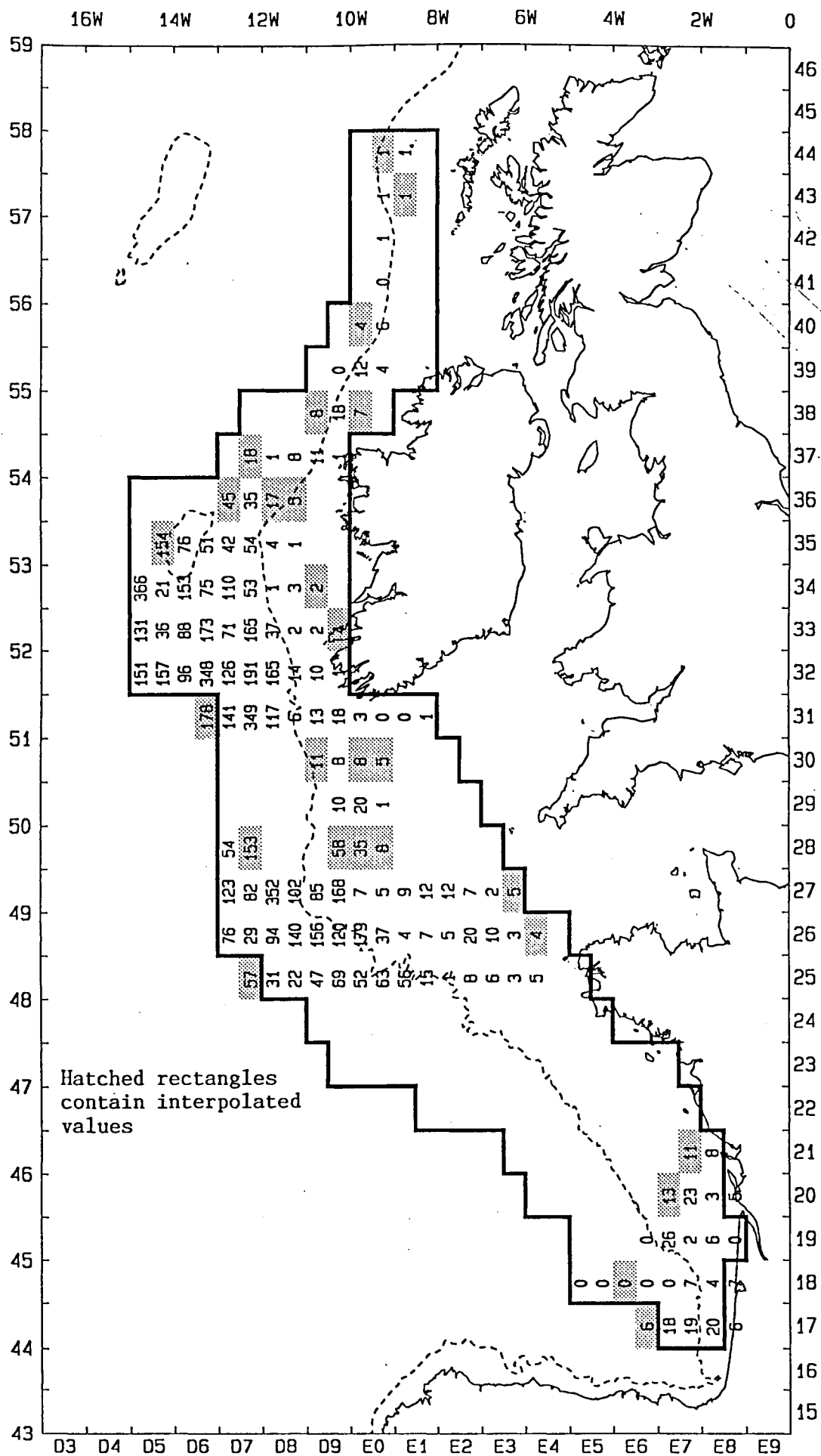
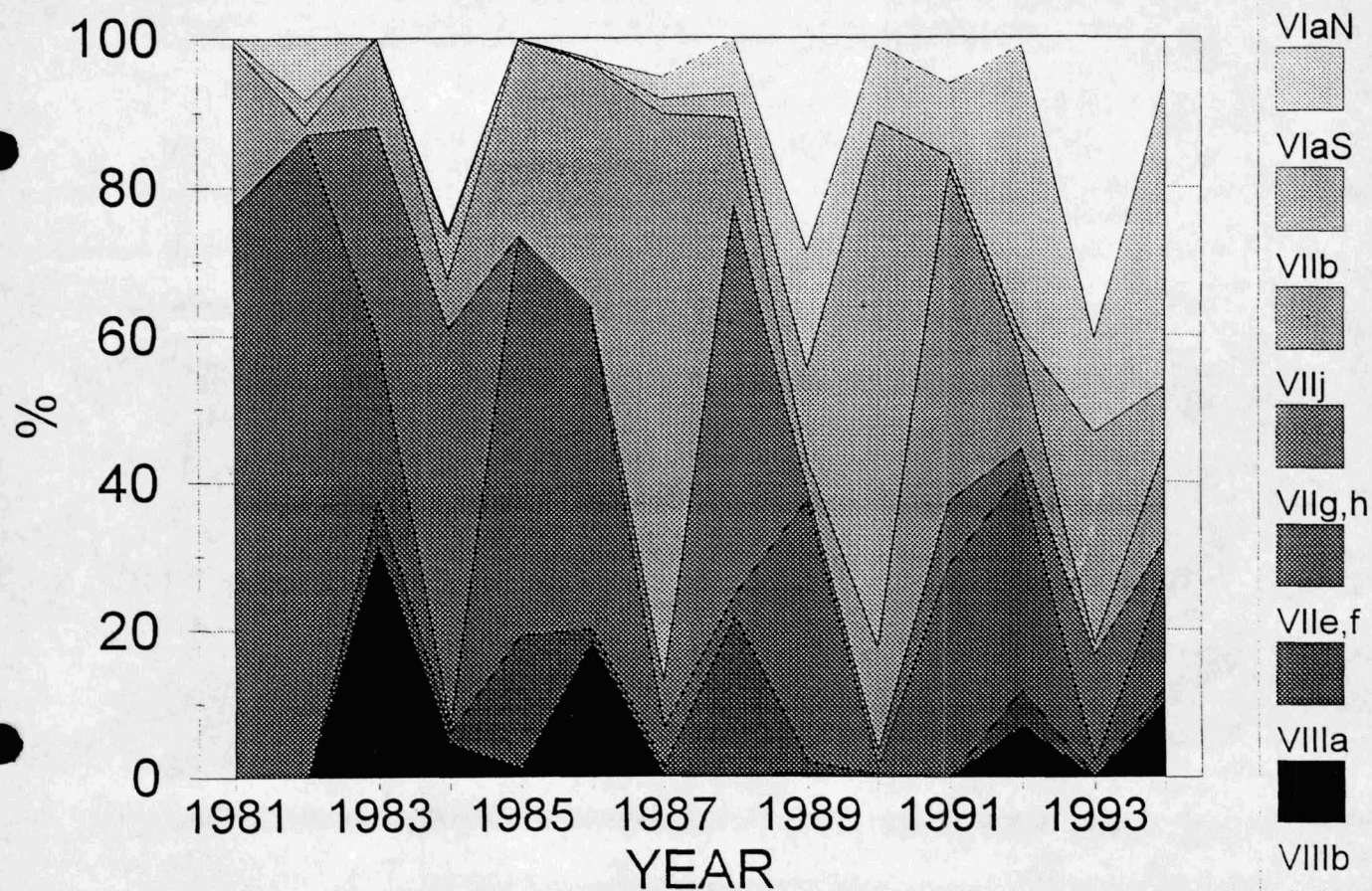


Figure 7e Mackerel nos/m²/day by rectangle from 1-31 May 1992.

Figure 8

Annual Changes in First-Winter Mackerel Distribution



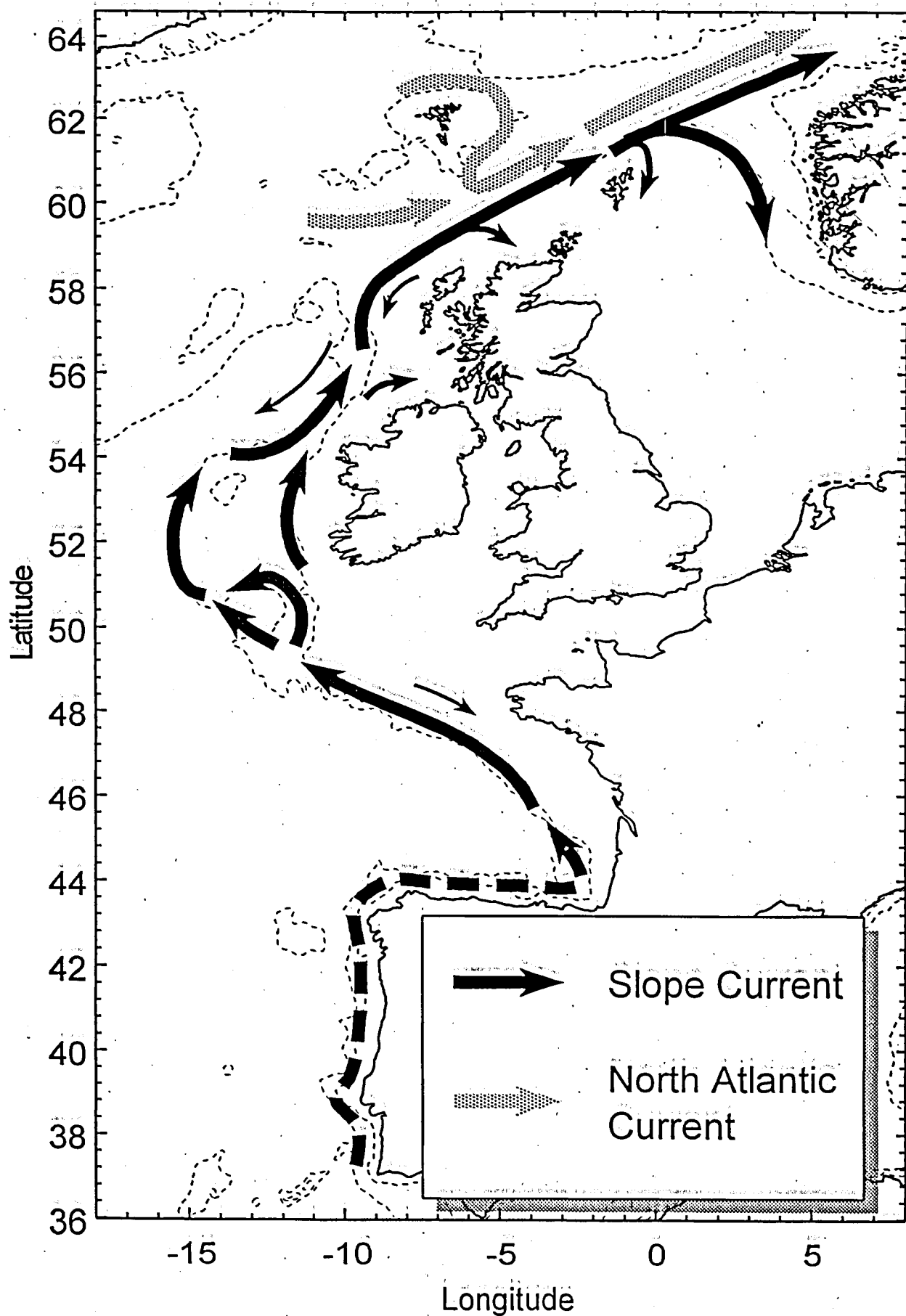
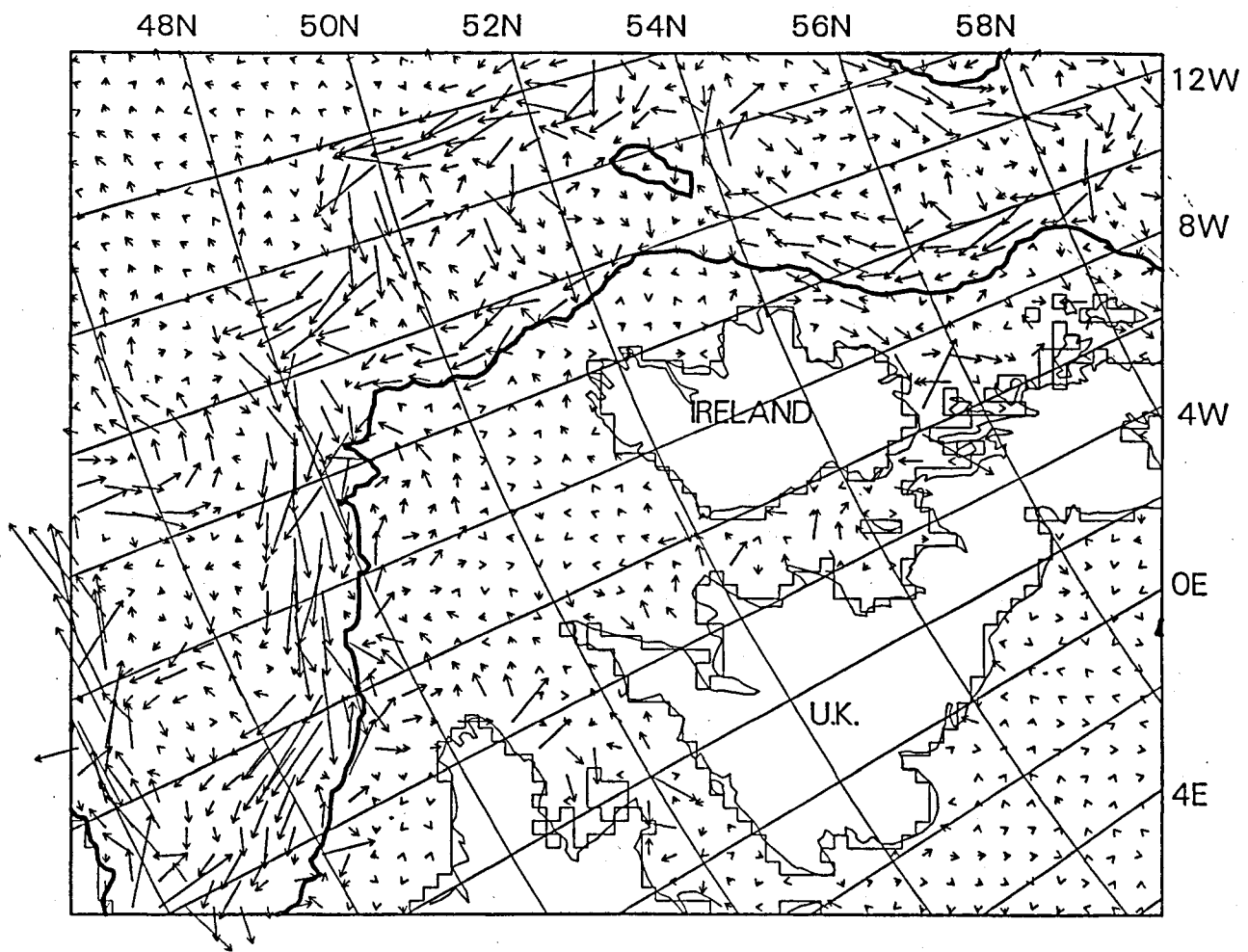


Figure 9 Schematic diagram of circulation near the shelf break.



AVERAGE VELOCITY 20 METERS, May 1976-94

Figure 10 Modelled circulation at 20 m depth.

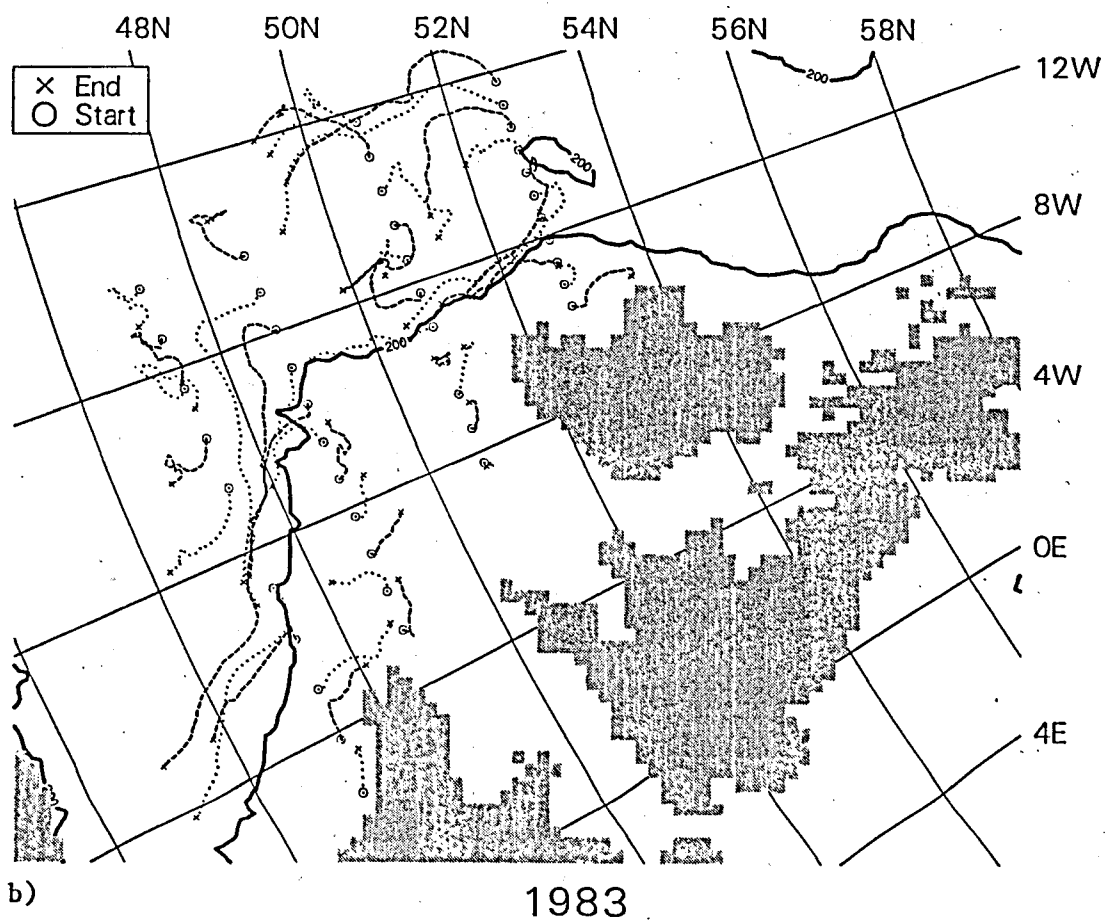
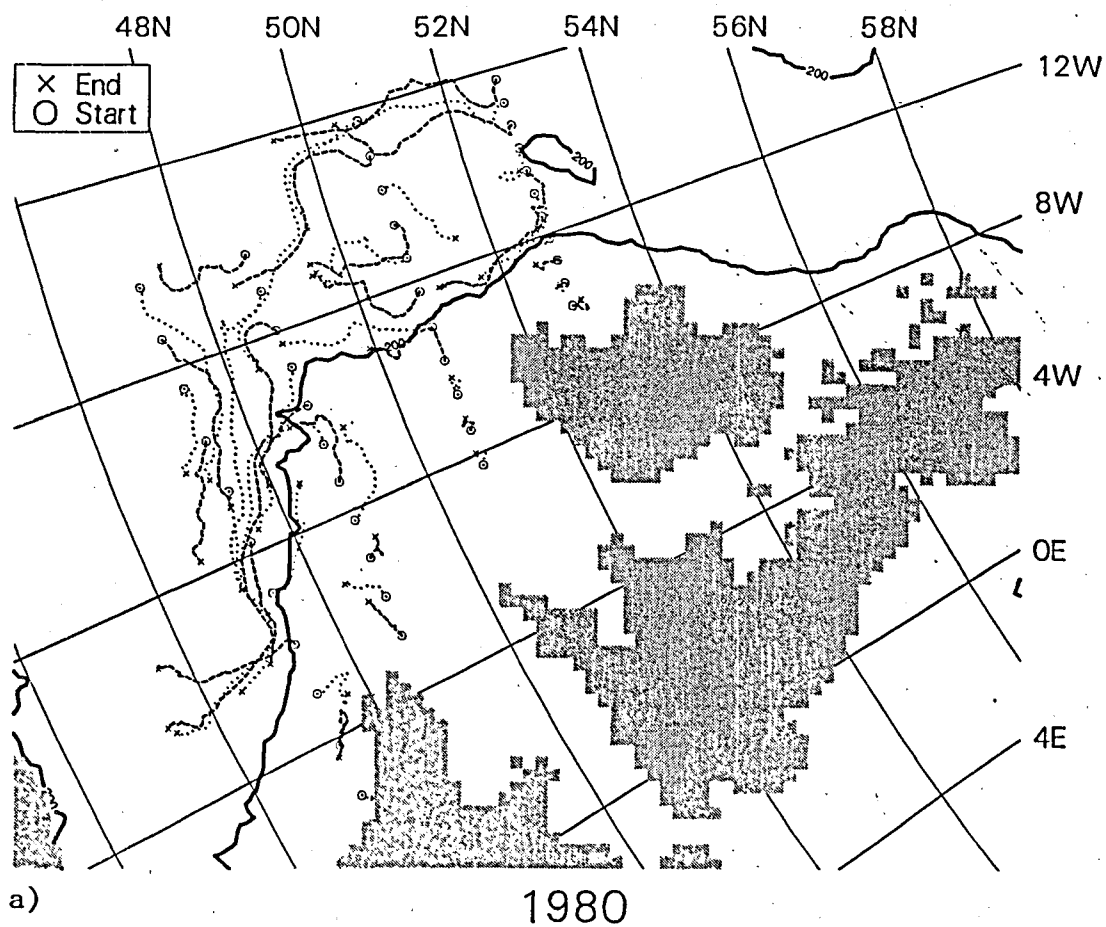


Figure 11 Spaghetti plots of 31 day transport (16 May - 15 June) at 20 m depth in five egg survey years.

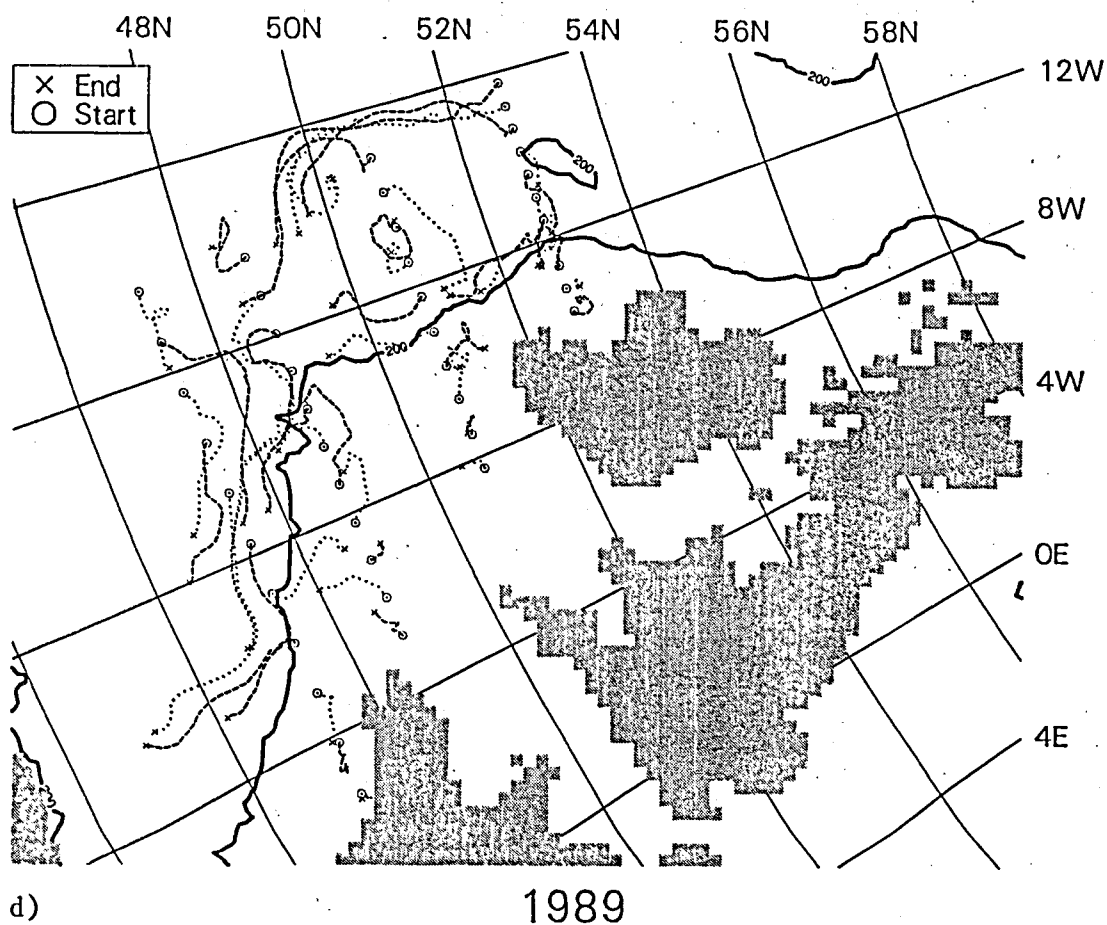
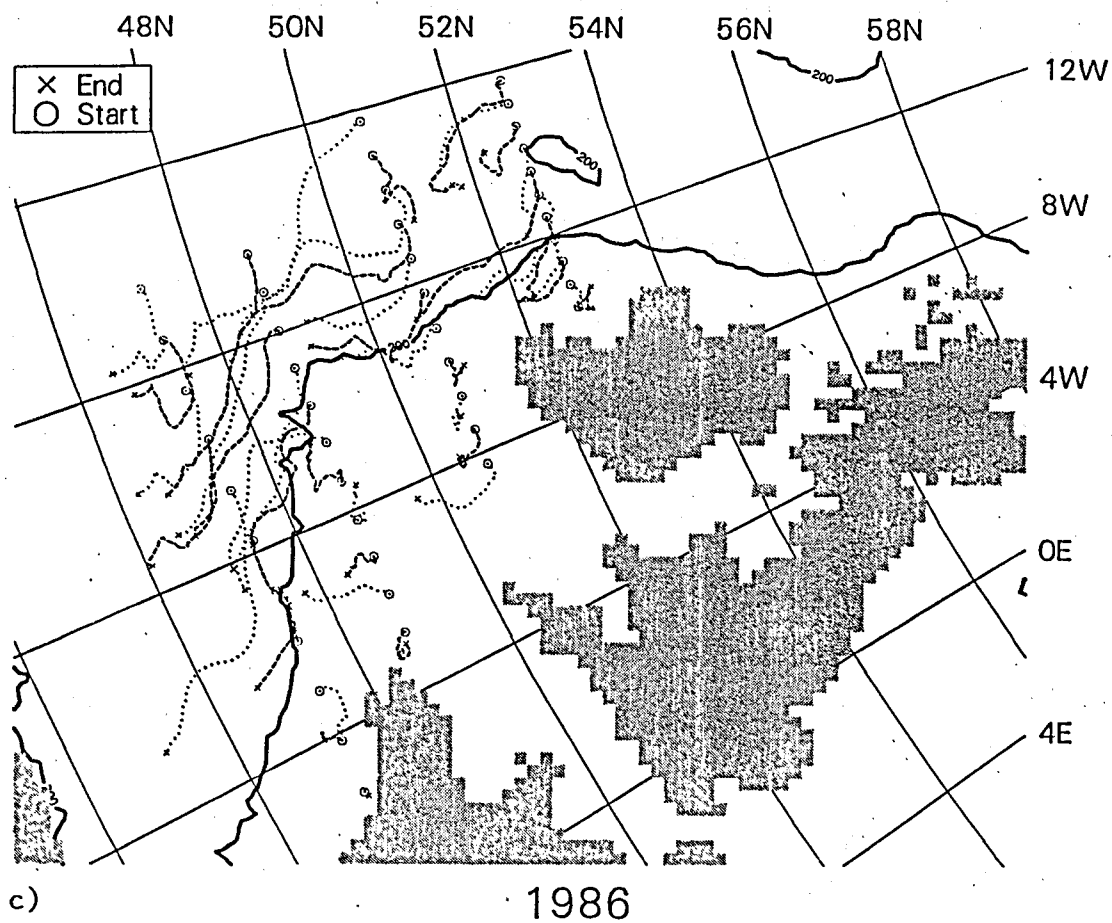


Figure 11 (cont)

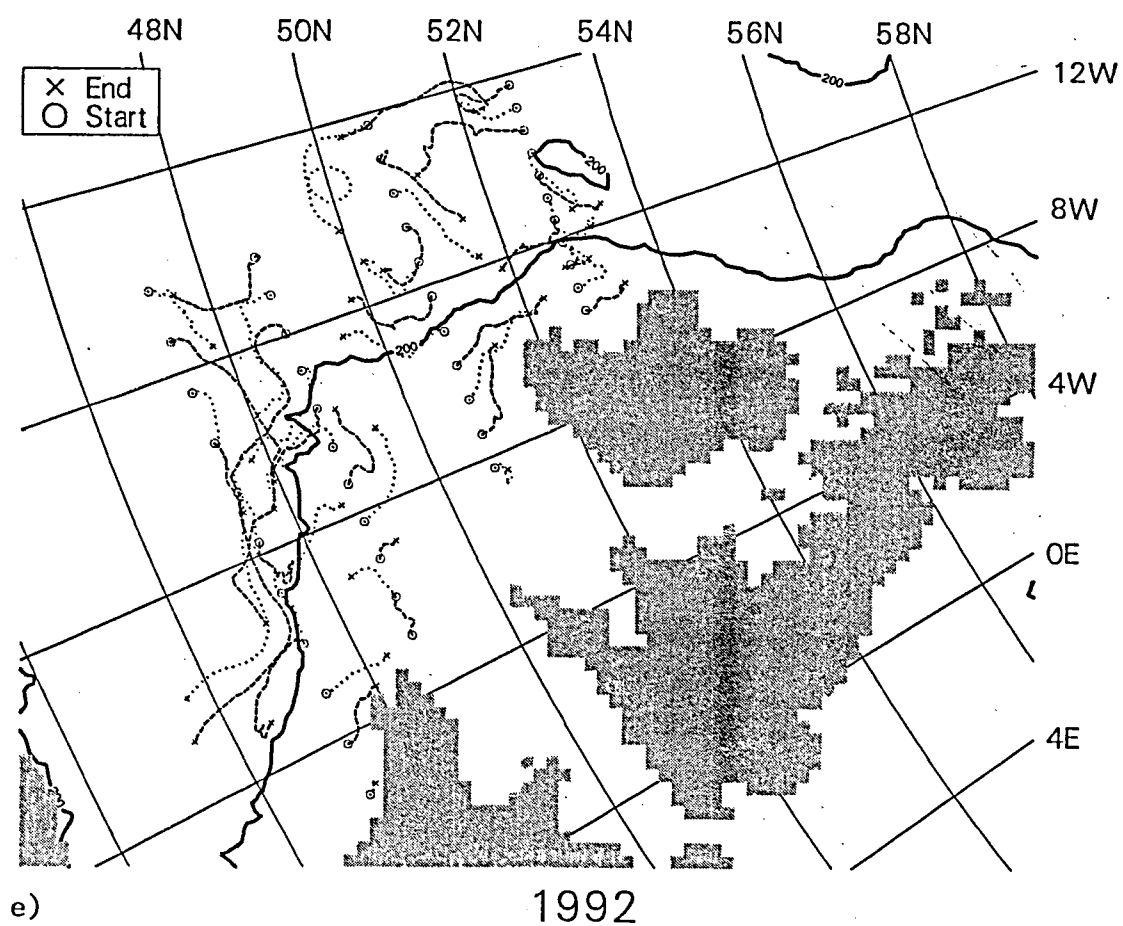


Figure 11 (cont)

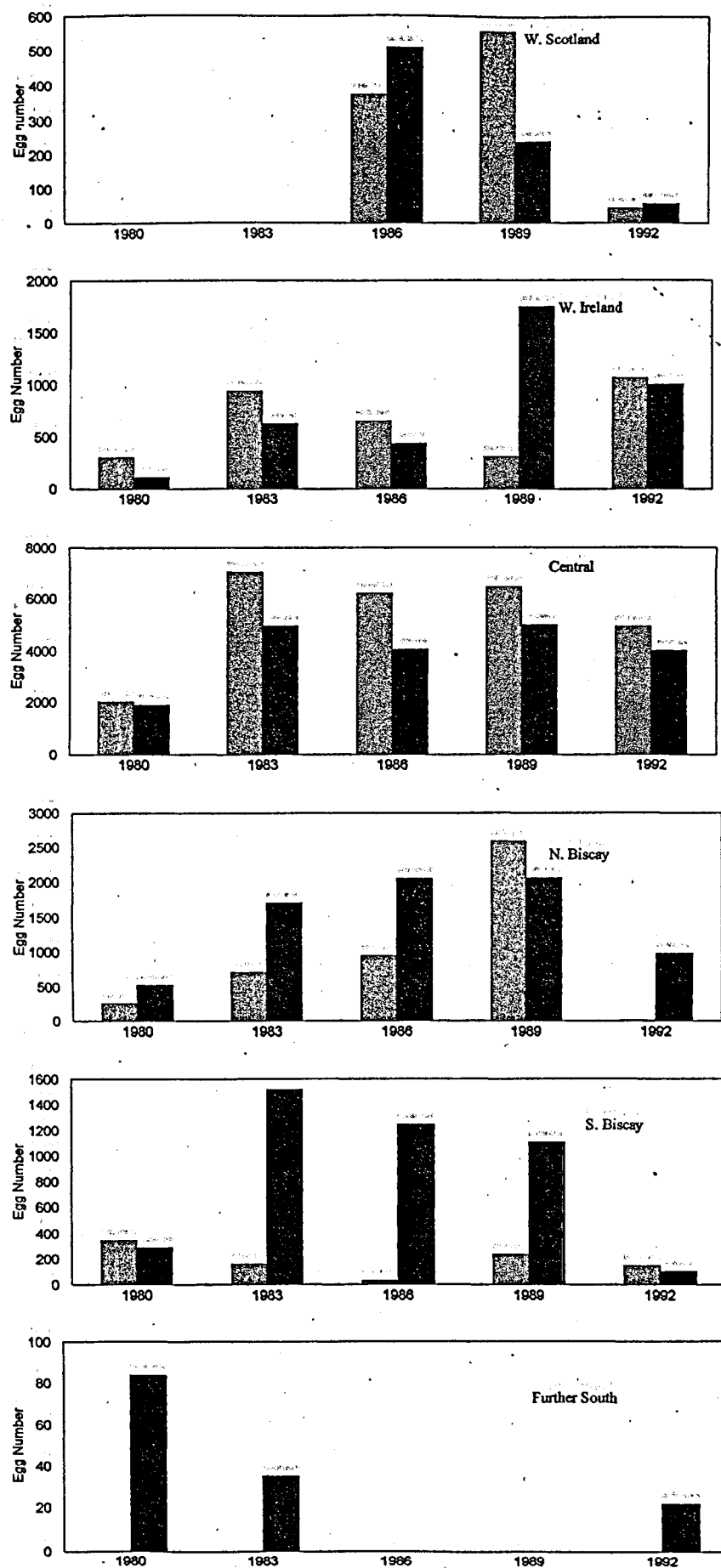
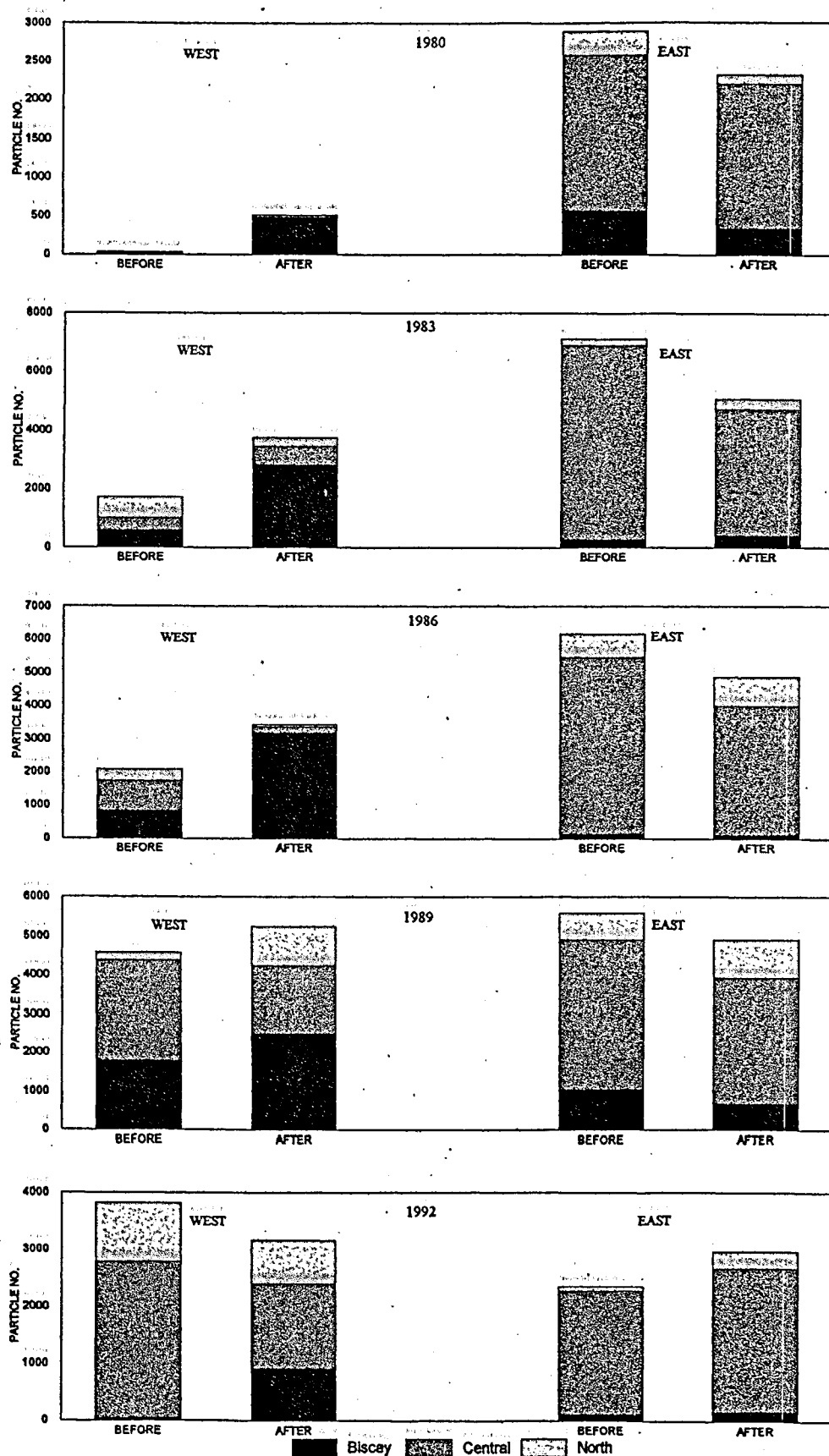


Figure 12

Changes in numbers of spawning particles in different latitude zones before and after 31 days transport. (For areas refer to Fig. 2).



Note on areas:

1. West: Biscay = $5a+6a$,
Central = $4a$
North = $2a+3a$
2. East: Biscay = $5b+6b$,
Central = $4b+d$
North = $2b+3b$

(see Fig. 2)

Figure 13

Changes in abundance of spawning particles before and after 31 days transport east and west of the shelf break.