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## INVESTIGATING THE COMPLEXITY OF SPATIO-TEMPORAL PATTERNS EVIDENCED IN THE TRIENNIAL MACKEREL EGG SURVEY DATA

D. Beare and D. Reid

FRS Marine Laboratory, PO Box 101, Victoria Road  
Aberdeen, AB11 9DB, Scotland, UK

### ABSTRACT

We investigate long-term, seasonal and spatial patterns in spawning activity by Atlantic mackerel (*Scomber scombrus*) along the continental shelf west of the British Isles. Stage I egg densities from eight international, triennial surveys (1977, 1980, 1983, 1986, 1989, 1992, 1995 and 1998) are modelled using non-parametric regression techniques. It is shown that seasonal and spatial patterns of egg abundance vary inter-annually. Long-term patterns of egg density are then compared to similar patterns of sea surface temperature. The authors then suggest that the overall long-term changes in stage I egg densities, which have fallen in the south of the study area (1977-1998) but risen in the north (1977-1998), have both been caused by the rising long-term temperature trend.

### INTRODUCTION

Stock sizes of pelagic fish, eg herring, are usually estimated using data from acoustic surveys, together with complimentary information from trawl surveys, market sampling and Virtual Population Analysis. Atlantic mackerel, however, have no swimbladder and are therefore comparatively difficult to detect using echosounding equipment.

Instead, spawning activity by females is used as an index of stock size (Lockwood et al., 1981). Surveys along the western continental shelf edge of stage I mackerel egg densities have been done triennially by a consortium of European marine laboratories since 1977. Once the egg (stage I) data have been collected and assimilated, an estimate of the total number of eggs spawned during a season can be made (the total annual egg production, TAEP). This figure can then be used to gauge the total number of sexually mature females and thenceforth the size of the stock (Gunderson, 1993; Hunter and Lo, 1993). Total annual egg production is estimated according to one of two procedures. In the first procedure, (The Traditional Method) stage I egg data are divided into crude space/time 'blocks' within which averages are calculated. These averages are then linearly extrapolated into unsampled 'blocks'. Where a block has no immediate neighbour, a zero is assigned. The second

method involves fitting **non-parametric** regression models (eg Generalised Additive Models, **GAMs**) to the data, where mean stage I egg densities are **modelled** as 'smooth' functions of various important 'predictor' variables, eg Julian Day and Distance from the 200 m contour (Borchers et al., 1997a; Borchers et al., 1997b).

Considerable recent research effort has been expended attempting to gauge the relative precision and bias of the different statistical procedures (Borchers et al., 1997a; Borchers et al., 1997b). The authors strongly support this, but also feel that the biologically interesting spatio-temporal patterns that emerge from such analyses are often insufficiently emphasised. It is debatable whether modern regression techniques have lower biases than the traditional methodologies, but they are certainly capable of revealing interesting information on patterns of spawning activity that may have been less accessible in the past. In this paper we set out to explore the output from **GAMs** fitted to stage 1 mackerel egg data with the objective of addressing specific scientific, rather than statistical questions.

Based on this we concentrate our investigations on the following aspects:

1. The seasonal pattern of spawning activity with location and between years;
2. The spatio-temporal pattern of spawning within and between years;
3. The influence of temperature.

## METHODS

Survey data from the eight triennial (1977, 1980, 1983, 1986, 1989, 1992, 1995 and 1998) surveys done so far were analysed in the present study. The locations are plotted in Figure 1. The surveys cover the same basic area (Fig. 1) but vary interannually in their detail. In the three earliest surveys (1977, 1980 and 1983) almost no data were collected north of 55°, after when **samples** were taken up to 60°N.

### Stage I Egg Density Data

Generalised Additive Models (**GAMs**) were used to model the stage I egg data for each separate survey. The framework for the analysis and protocol for the model-selection routines are based on methods developed at St Andrews University (see Borchers et al., 1997a, b). The following four covariates were used to predict stage I egg density: *Cdist* (distance from 200 m depth contour), *Ndist* (distance along 200 m depth contour), Week, and log-transformed Bottom *Depth*. Week Number was used in preference to Julian Day (cf. Borchers et al., 1997a,b), since it also captured detail of temporal trends but had the advantage of being less demanding on computer processing time. Initially a 'full-model' was fitted to the egg density data which included all of the covariates, *Cdist*, *Ndist*, Week and Depth, estimated either as linear terms, or as spline smooths with four degrees of freedom. The products of all pairs of the covariates were also included to allow interaction to occur. A standard step-wise regression procedure then found the most economical subset of the covariates by minimisation of the Akaike Information Criterion. All the models assume that stage I egg data arise from the Negative Binomial distribution which is often used for modelling the mean/variance ratio typical of aggregated count data such as these (Venables and Ripley, 1994; Lindsey, 1995). The edges of the survey were **constrained** in space and time using zeros.

## Sea Temperature at 20 m Data

Temperature measurements are taken contemporaneously with the stage I egg data and were fitted to the same four covariates, eg Week, Depth, *Cdist* and *Ndist*. Ordinary linear models were found to be adequate for describing dependence in the temperature data. The most economical subsets of the regressors were again found by minimising the AIC criterion.

## RESULTS

Parameters from the models for both stage I egg density and sea-temperature were used to interpolate over a grid of the four predictors (Week, Depth, *Cdist*, *Ndist* and their 2-way interactions) providing temporally evolving spatial surfaces. Those for the 1998 stage I mackerel eggs are shown in Figure 2, and sea temperature at 20 m in Figure 3. The long-term, seasonal and spatial patterns evidenced within these modelled surfaces were then explored using visual methods.

### Long Term Trends

#### Total annual egg production

The volume under each spatio-temporal surface represents a measure of the total annual egg production (TAEP) which is important in the stock assessment procedure since it is directly related to the stock of adult females. TAEPs were calculated for each of the eight triennial surveys using GAMs. The TAEP curves (Fig. 4A) for the 1980, 1983, 1989 and 1995 datasets have remarkably similar shapes (Fig. 4A). The 1977 and 1998 surveys had relatively low TAEP, while spawning in 1992 appeared to start much earlier than usual. The exceptionally late onset of spawning in the 1986 data is probably an artefact, since surveying activity was delayed in that year. Long-term trend in TAEP (Fig. 4B) increased overall between 1977 and 1992 since when it has declined.

#### Sea-temperature

Average sea surface temperatures (eg Fig. 3) were calculated and the output plotted (Fig. 5A). In 1977, for example, minimum average temperatures were just below 8°C while the average maximum in week 30 was ca 16°C. Long-term trend in average temperature is characterised by the regression line (Fig. 5A) which shows a gradual overall rise. Nevertheless, there are other possibly more important features in the data than a simple rising trend. Average temperature ranges were much greater in 1986, 1989 and 1992 than those observed during the other five surveys (1977-1983 and 1995-1998). In 1989, for example, minimum average temperatures were as low as 7°C in late winter (February), and as high as 18°C by late summer (August). This information was summarised by gradients representing the rate of temperature increase between weeks 5-30 (Fig. 5B). The magnitude of the gradients peaked in 1989 and 1992 when sea temperatures rose at a rate of nearly 0.5°C per week. There is a clear positive correlation between the rate of average temperature increase and TAEP (see Figs 4 and 5).

#### Stage I egg density and temperature along 200 m contour

Spawning activity by Atlantic mackerel is concentrated along the 200 m bathymetric contour (Fig. 2). To investigate the impact of location on perception of long-term trend, arbitrary points were selected along the 200 m contour (Fig. 6, Top Left) at which long-term trends for Weeks 16, 21 and 26 are plotted. Only data below 55N were considered, since the 1977

and 1980 surveys did **not** go beyond that point (see Fig. 1). Starting at 54.5°N, 10°E and moving south along the 200 m contour (Fig. 6) until ca 52.5°N, 11.5°E stage I egg densities increased steadily, irrespective of the time of year (season). Troughs in egg density were observed in the earlier part (Week 16) of the year in the 1986 survey and in the later part of the year (Week 26) in the 1983 survey. Further south, at ca 52°N, 11.5°E, and long term trends in different parts of the year diverge. Egg densities in Week 21 fell slightly, whereas in Weeks 16 and 26 there was no obvious trend.

Analogous plots for sea temperature along the 200 m contour are plotted in Figure 7. In the southern part of the 200 m contour line, between 50.5°N, 10.5°E and 47°N and 4°E, long-term trends in **sea** temperatures were well-correlated, with a minimum in 1986 and a maximum in 1989/1992. Further north the temperature time-series exhibit seasonal differences in long-term trend. In Week 16, for example, minimum temperatures occurred in 1986 whereas in Week 26, they occurred during the 1983 survey. This phenomenon also happens in the stage I egg density data (Fig. 6). Overall, sea-temperature has risen over the whole area between 1977 and 1998.

Long-term trends in spatial patterns were compared using 'anomaly plots' where egg densities (stage I) or temperatures at each grid node were compared to the mean level at that point for all eight surveys (1977, 1980, 1983, 1986, 1989, 1992, 1995 and 1998). Positive anomalies (white) represent grid nodes where the mean stage I egg density was higher than the mean 1977-1998 value, while negative anomalies (black) represent those points in space and time that had lower average densities than the mean 1977-1998 level (Fig. 8). In 1977 and 1980 there were high positive stage I egg density anomalies in the south and inshore (Fig. 8) which contrasts with the patterns in 1995 and 1998 when positive anomalies occurred in the north and further offshore. The spatio-temporal surfaces for the 1986, 1989 and 1992 surveys were all positive and there was comparatively little spatial heterogeneity. This means that the overall level of egg density in those years was high; and the shapes of each surface were similar to the average.

## Seasonal Patterns

### Seasonal patterns along the 200 m contour

The plots of TAEP production (Fig. 4) are summaries of the overall seasonal change each survey. Each point on the TAEP curve represents the stage I egg density per square metre of seabed summed over the entire survey area (approx 648,000 km<sup>2</sup>) which is a crude summary of the seasonal dependence. By selecting specific points in the survey area, changing patterns of seasonality can be explored in the absence of any spatial confusion. Variations in the shape of the seasonal egg density pattern at 11 arbitrary points along the 200 m contour for each of the eight surveys are shown in Figure 9. The shape of the seasonal pattern changes both with position along the 200 m contour and between surveys (Fig. 9). The pattern for any particular point is generally unimodal, although there was some bimodality in the 1992 and 1998 surveys. In 1992, the relative magnitude of the two seasonal peaks changes along the 200 m contour. In the north, the second peak in the year is larger than the first and vice versa in the south (Fig. 9).

## DISCUSSION

Confident interpretation of the stage I egg density data from the eight triennial surveys is compromised by a variety of important considerations which cannot be ignored. Firstly the

data are extremely **sparse** for summarising a quantity as variable as stage I egg density over such a large area of sea. There are approximately only 1,000 observations for each of the eight surveys which are being used to estimate daily egg production over an area in excess of 648,000 km<sup>2</sup>. Confounding or non-random sampling in space and time in the data also causes problems which are difficult, if not impossible, to ameliorate. The spatial extent of the survey has changed between years and, in most of the eight surveys, there are long periods of time when no sampling was done at all (Fig. 2). Sampling activity typically begins each year in the south and ends in the north which probably causes bias. In 1977, 1980 and 1983 there are no data at all north of 55°N making comparisons with other years impossible. In 1986, sampling began later in the year than usual (Week 15) and the late, rapid rise of stage I egg densities observed in the data for that year (Fig. 4A; Fig. 8) is an **artefact**.

Assumptions about the start, end and spatial boundaries of spawning activity have been made in the current study and it is impossible to know how seriously these affect the interpretation of long-term, seasonal, and spatial trends we observe in the model outputs. The assumptions are made by using artificial zeros which are positioned around the survey area at points in space and time by expert scientists with detailed biological knowledge about the extent of spawning by mackerel. Unfortunately, the results described here suggest that spawning behaviour by mackerel varies interannually and that such assumptions may not always be correct. There are no sensible solutions to such problems, but our analysis has nevertheless been worthwhile and useful scientific information has been extracted which would have been less accessible to 'Traditional' methods.

There is an overall long-term trend in the abundance of stage I egg density. It peaked in 1989 and 1992. The pattern of long-term increase, however, varies across the survey area. From 1977-1983 stage I egg abundance tended to be highest in the south, while in the late 1980s and 1990s it was highest in the north. Temperature has increased steadily overall between 1977 and 1998. The winter of 1988-1989 was unusually mild (Lindley et al., 1990) although this is not clearly reflected in our data (Fig. 5) and positive temperature anomalies persisted throughout the rest of the year (Northcott, 1989, 1990). The winter of 1997/1998 was also exceptionally warm and February air temperatures (see Fig. 5) were +3°C higher than the long-term (1961-1990) average (Edwards et al., 1997).

In simplistic terms, temperature ultimately controls the broad scale distribution of most species of plants and animals. What is more interesting, however, is how fluctuating temperature within the geographic range of a particular species might modulate its abundance, growth and reproductive activity. Unfortunately the current temperature data are as sparse and as confounded in space and time as the stage I egg density data and it is impossible to propose concrete mechanistic links between the two quantities. A further consideration is that the temperature measurement itself is involved in the calculation of stage I egg density data that are used to estimate spawning activity, (see Fig. 2). This means that the temperature and egg density data explored in this study are not independent of each other, and you would expect them to be related.

In spite of such considerations the results suggest *ad hominem* that sea temperature is an influential factor in regulating spawning activity by mackerel at the margins of its temperature range (both temporally and spatially of spawning): that is to say, at the beginning of the year, and in the northerly and southerly edges of the survey region (Corten and van de Kamp, 1992; Walsh et al., 1995). Long-term trends in stage I egg densities tended to be positively correlated with temperature in the north, constant in the centre and negatively correlated in the south (Fig. 6). Temperatures of about 14-16°C appear to be critical to mackerel spawning. [Note: These temperatures are much higher than the 7.75-9°C suggested as

general preferenda of the species by Walsh et al. (1995)]. Above this range and stage I egg densities are low, and below this range stage I egg densities are also low. Such relationships have been documented for other fish species. The recruitment responses of cod, for example, are sensitive to temperature depending on their geographic location (O'Brien et al., 2000).

This finding has serious implications against the backdrop of global warming and suggests that, if the warming trend continues, mackerel spawning activity will move steadily further north along the 200 m contour.

## ACKNOWLEDGEMENTS

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TABLE 1

Best models for stage I egg density for surveys 1977-1998.

Year	Most economical subset based on Akaike Information Criterion
1998	$S(\text{Week}) + \text{Depth} + \text{Cdist} + S(\text{Ndist}) + S(\text{Week} * \text{Cdist}) + S(\text{Week} * \text{Ndist}) + (\text{Depth} * \text{Cdist}) + S(\text{Depth} * \text{Ndist}) + (\text{Ndist} * \text{Cdist})$
1995	$S(\text{Week}) + S(\text{Depth}) + \text{Cdist} + S(\text{Ndist}) + S(\text{Week} * \text{Depth}) + (\text{Week} * \text{Cdist}) + (\text{Week} * \text{Ndist}) + (\text{Depth} * \text{Cdist}) + (\text{Depth} * \text{Ndist}) + (\text{Ndist} * \text{Cdist})$
1992	$S(\text{Week}) + \text{Depth} + \text{Cdist} + S(\text{Ndist}) + S(\text{Week} * \text{Depth}) + S(\text{Week} * \text{Cdist}) + S(\text{Week} * \text{Ndist}) + S(\text{Depth} * \text{Cdist}) + (\text{Depth} * \text{Ndist}) + (\text{Ndist} * \text{Cdist})$
1989	$S(\text{Week}) + \text{Depth} + \text{Cdist} + S(\text{Ndist}) + S(\text{Week} * \text{Depth}) + S(\text{Week} * \text{Cdist}) + S(\text{Week} * \text{Ndist}) + (\text{Depth} * \text{Cdist}) + (\text{Depth} * \text{Ndist}) + S(\text{Ndist} * \text{Cdist})$
1986	$S(\text{Week}) + S(\text{Depth}) + \text{Cdist} + S(\text{Ndist}) + S(\text{Week} * \text{Depth}) + (\text{Week} * \text{Cdist}) + S(\text{Week} * \text{Ndist}) + S(\text{Depth} * \text{Cdist}) + S(\text{Depth} * \text{Ndist}) + (\text{Ndist} * \text{Cdist})$
1983	$S(\text{Week}) + S(\text{Cdist}) + S(\text{Ndist}) + S(\text{Week} * \text{Cdist}) + S(\text{Week} * \text{Ndist}) + (\text{Depth} * \text{Cdist}) + S(\text{Depth} * \text{Ndist}) + (\text{Ndist} * \text{Cdist})$
1980	$\text{Week} + S(\text{Depth}) + \text{Cdist} + S(\text{Ndist}) + S(\text{Week} * \text{Depth}) + (\text{Week} * \text{Cdist}) + S(\text{Week} * \text{Ndist}) + (\text{Depth} * \text{Cdist}) + (\text{Depth} * \text{Ndist}) + (\text{Ndist} * \text{Cdist})$
1977	$S(\text{Week}) + \text{Depth} + S(\text{Ndist}) + S(\text{Week} * \text{Depth}) + (\text{Week} * \text{Cdist}) + S(\text{Week} * \text{Ndist}) + S(\text{Depth} * \text{Cdist}) + S(\text{Depth} * \text{Ndist})$

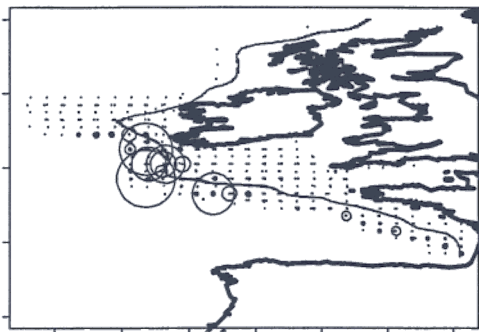


## FIGURE LEGENDS

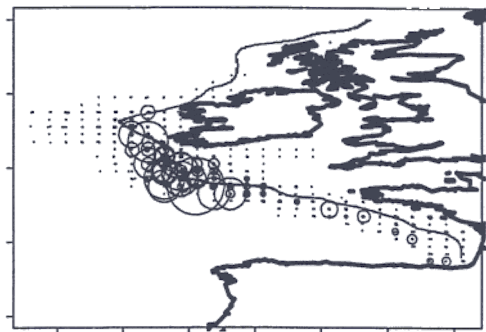
- Figure 1      Location of stage I mackerel egg density data 1977-1998.
- Figure 2      Stage I mackerel egg densities west of the British Isles in 1998 from weeks 5-30. Points are raw data; solid white line is 200 m depth contour. Bottom row, 3rd plot is total annual egg production curve; bottom row, 4th plot is raw egg density data vs week number. Dark grey = high egg density; white = low egg density.
- Figure 3      Sea temperature at 20 m west of the British Isles in 1998 from weeks 5-30. Points are raw data; solid line is 200 m depth contour. Bottom row, 3rd plot is average temperature each week; bottom row, 4th plot are temperature data vs week number. Dark grey = high temperature; white = low temperature.
- Figure 4      A) Total annual egg production curves 1977-1998. B) Long-term change in total annual egg production 1977-1998. Trend is summarised with a variable-span smoothing algorithm.
- Figure 5      A) Solid lines: average weekly sea surface temperature 1977-1998. Broken lines: change in temperature minima and maxima 1977-1998. B) Rate of change of temperature each week 1977-1998.
- Figure 6      Long-term trend in stage I mackerel egg densities at 18 arbitrary locations (see top left map) for weeks 16, 21 and 26 along 200 m depth contour 1977-1998.
- Figure 7      Long-term trend in temperature at 18 arbitrary locations (see top left map) for weeks 16, 21 and 26 along 200 m depth contour 1977-1998.
- Figure 8      Stage I egg density anomalies from 1977-1998 average for week 26.
- Figure 9      Interannual variation in seasonal pattern at 11 arbitrary (see top left map) locations along 200 m depth contour.

# Location of Stage Mackerel Egg Data

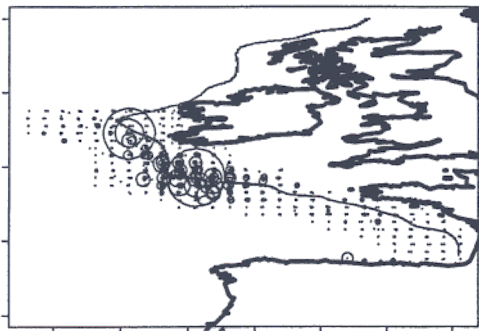
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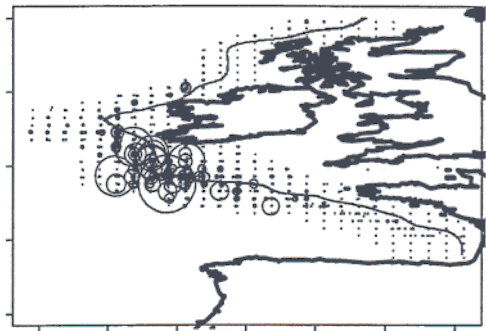
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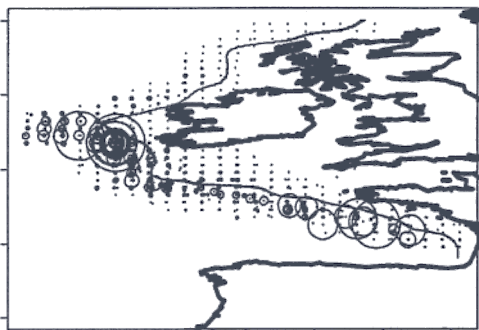
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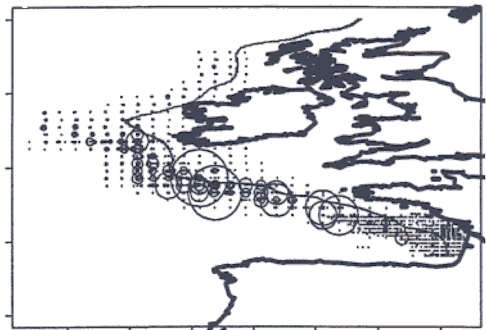
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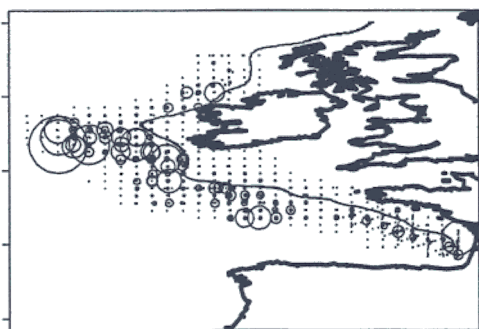
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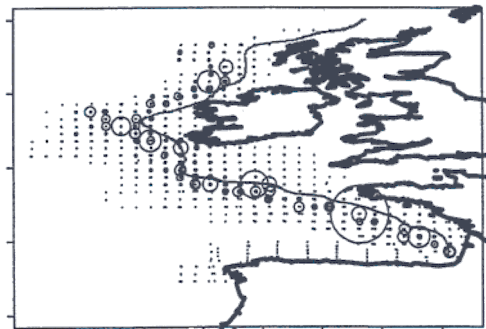
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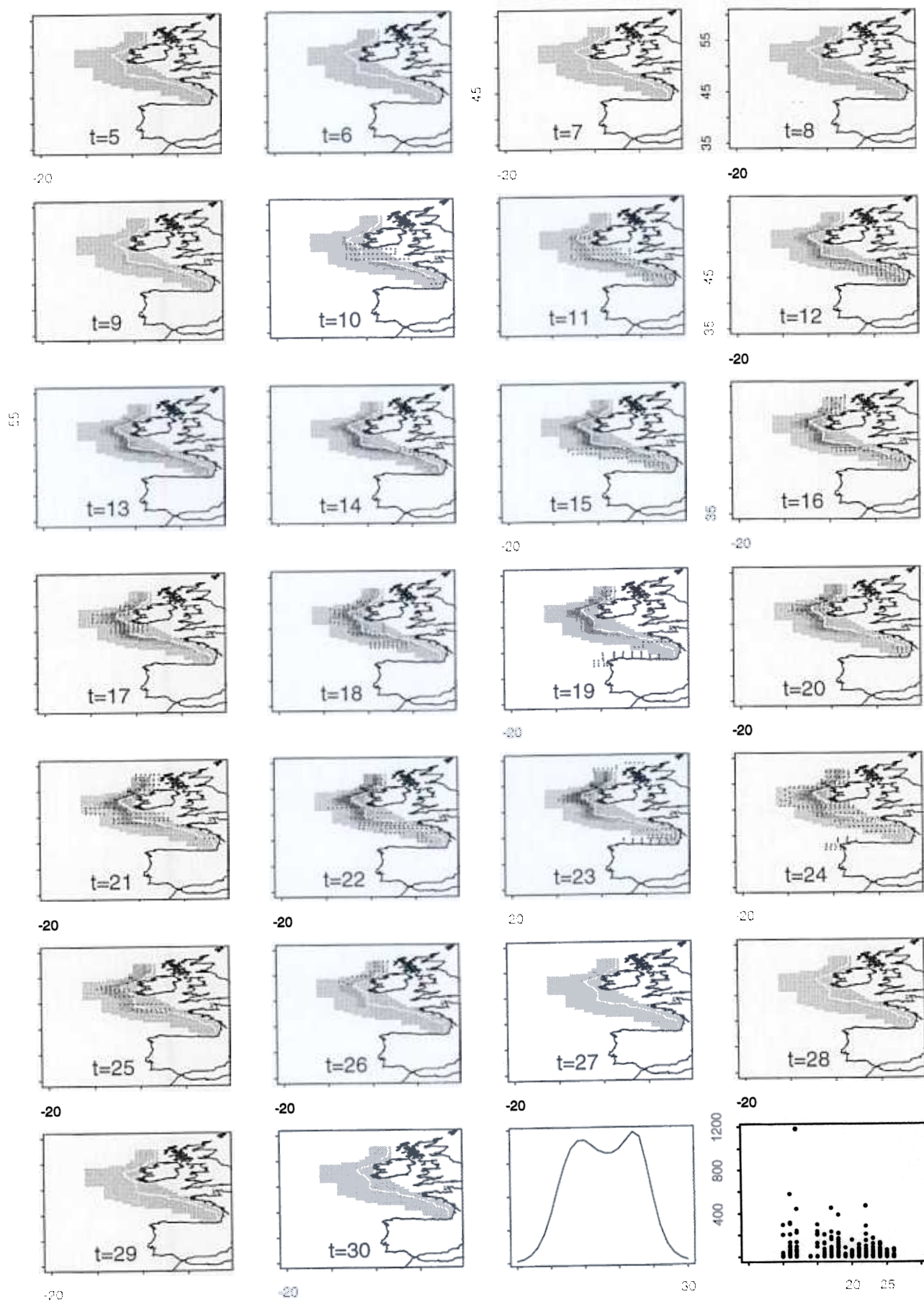
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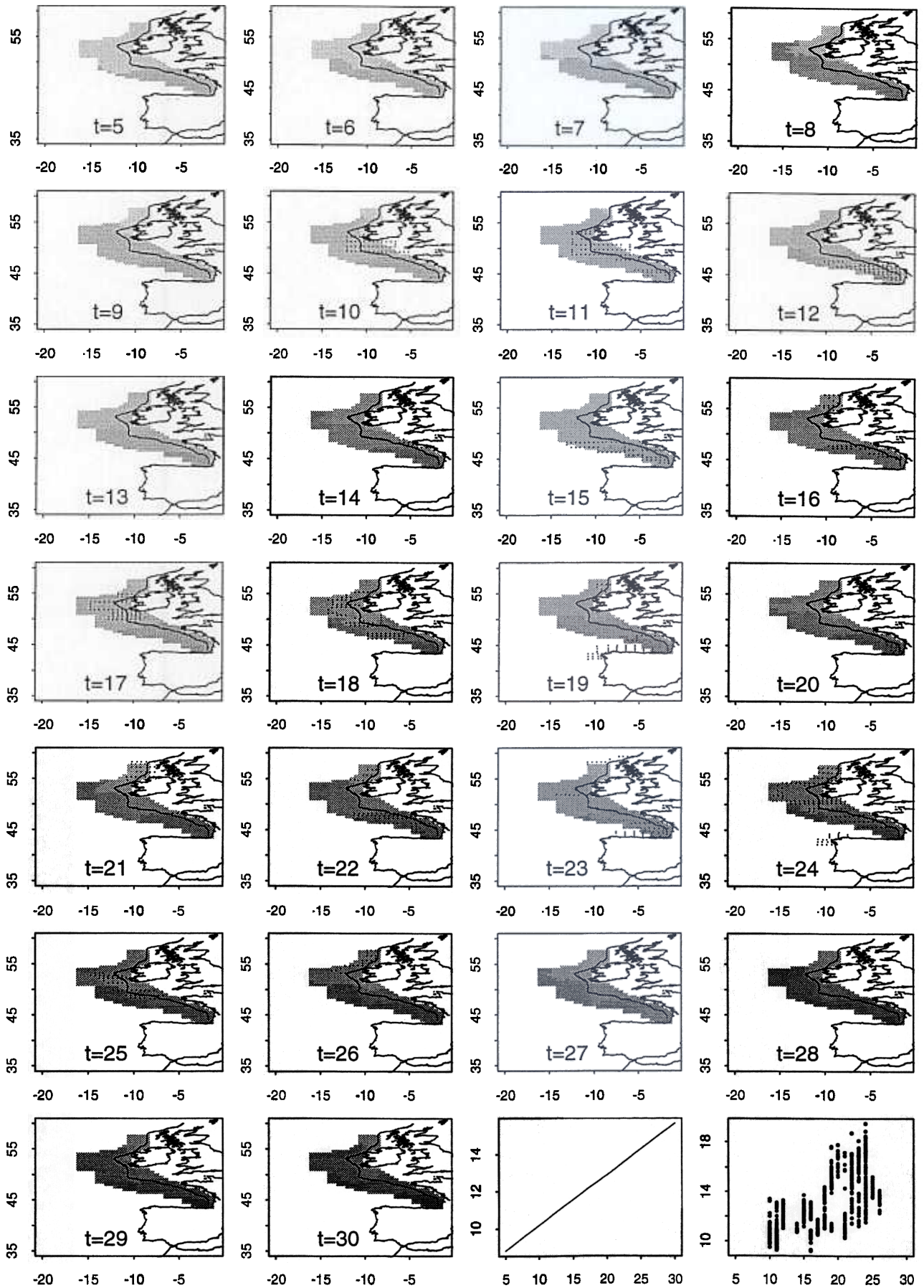
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Longitude

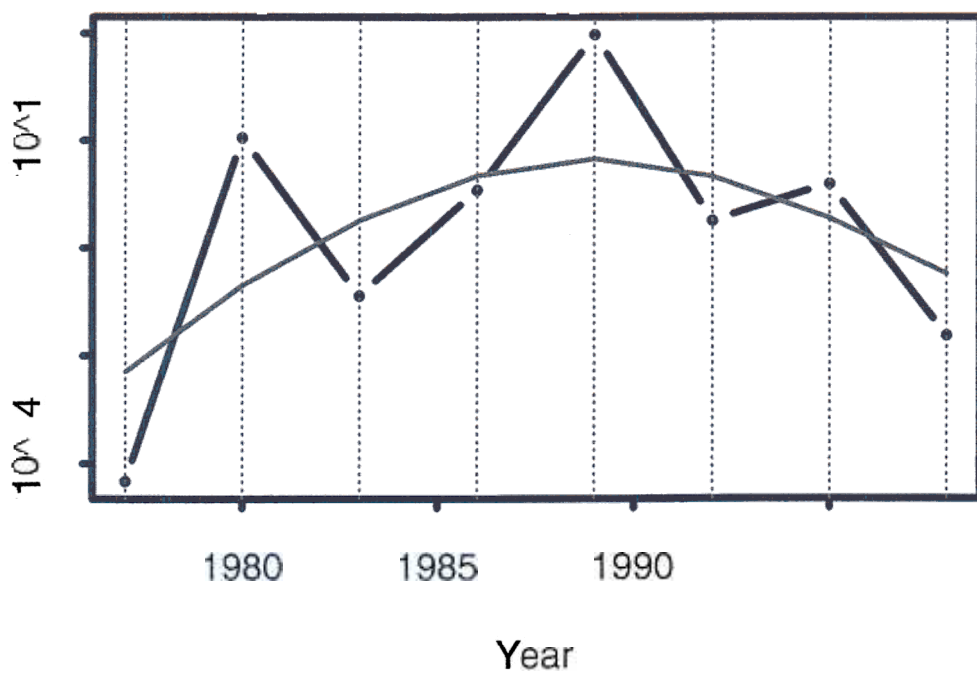
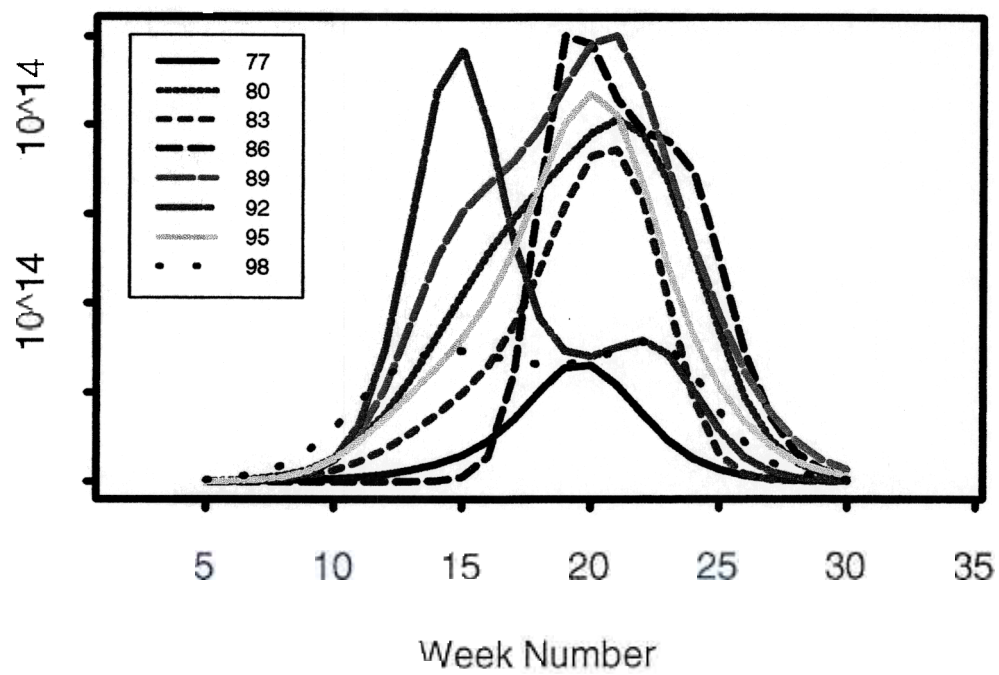
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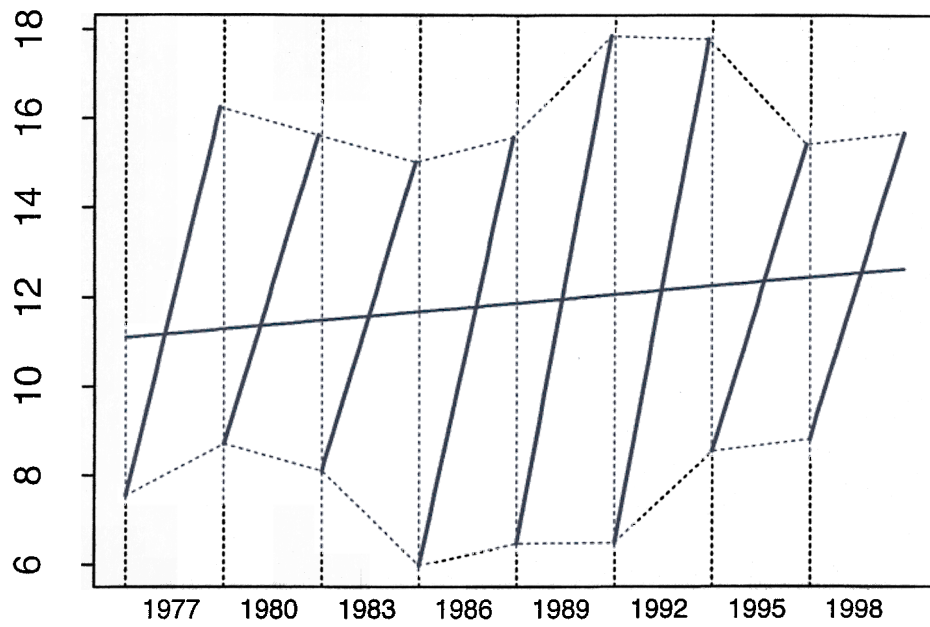
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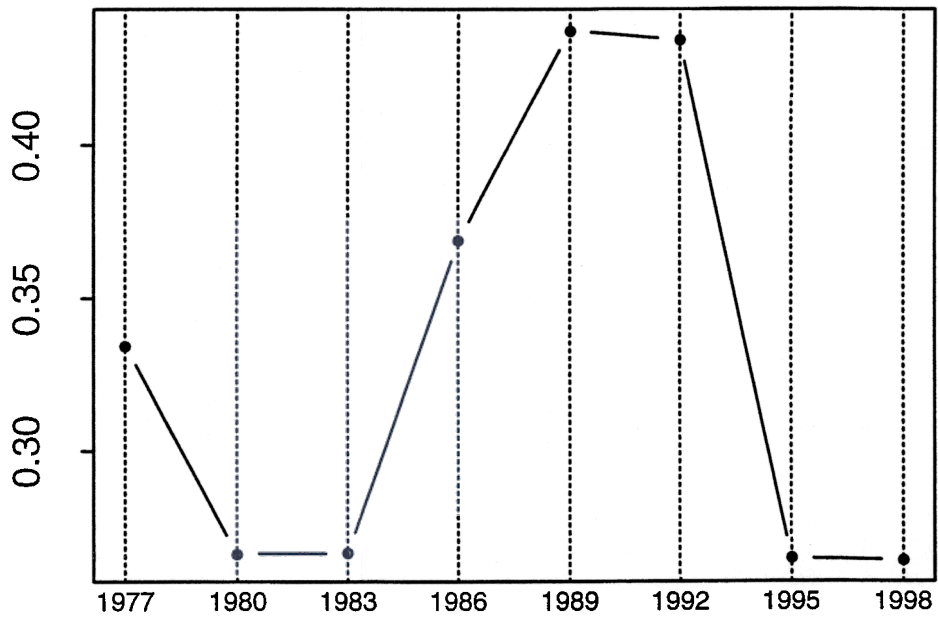




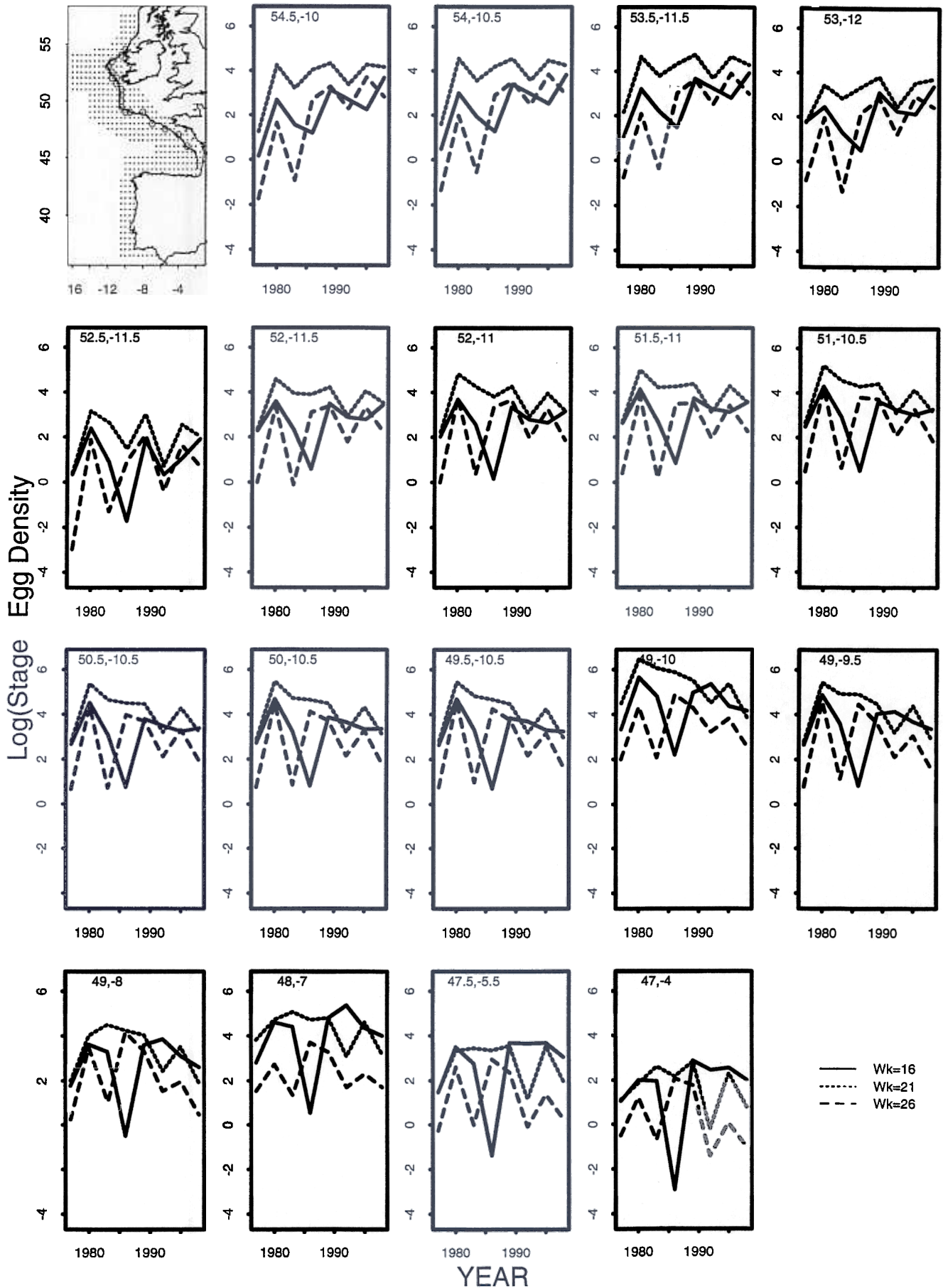
### Average weekly SST



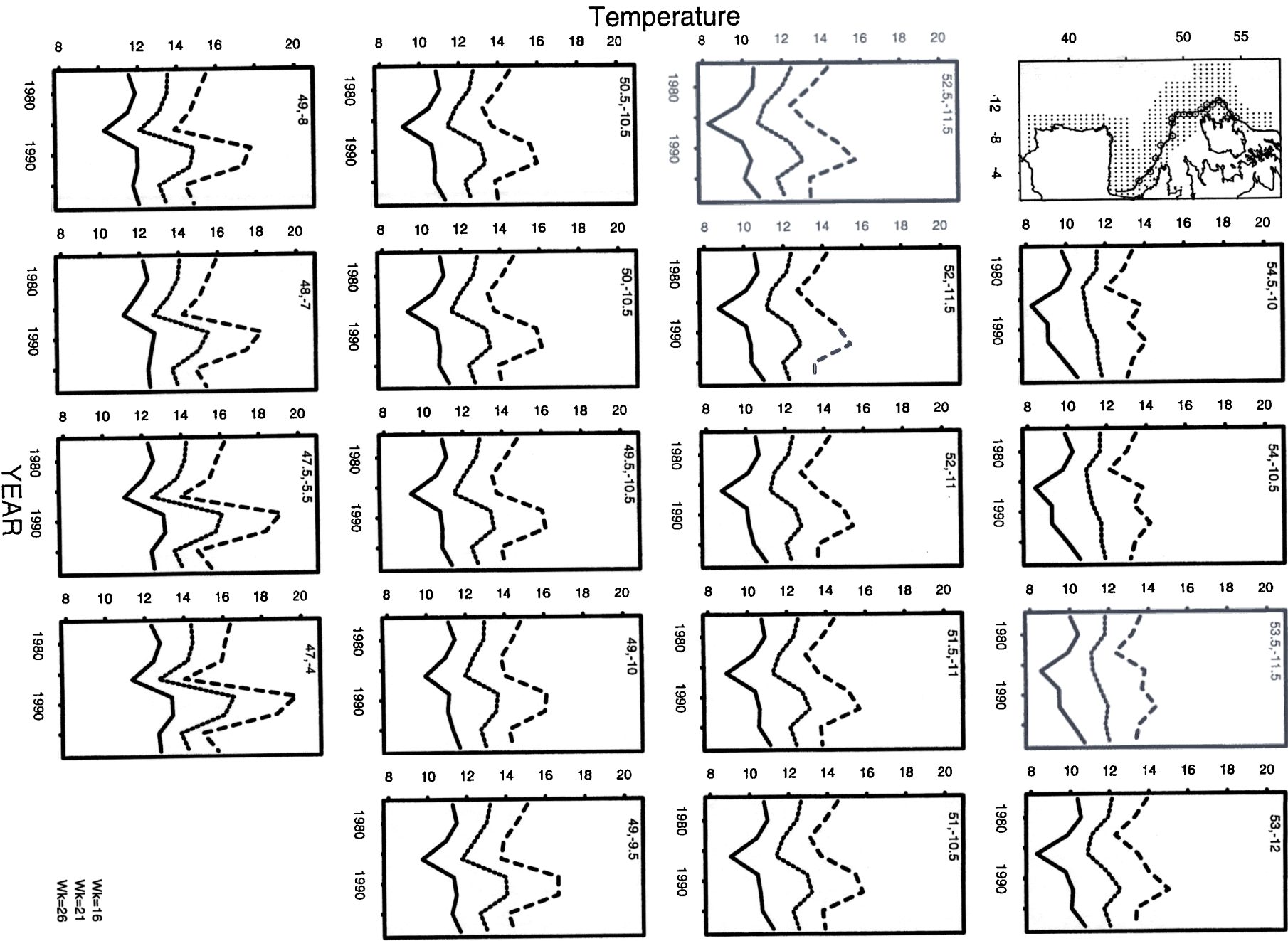
### Weekly rate of increase of SST



# Long-term trend: Stage Mackerel Eggs along 200m contour



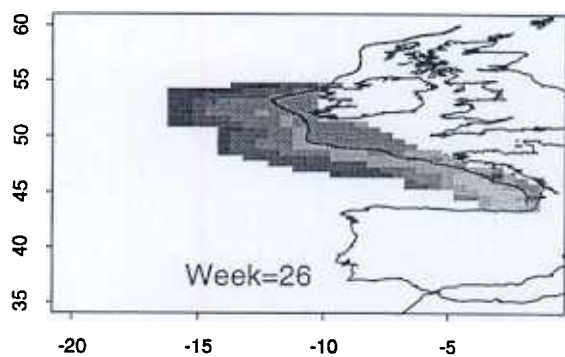
Long-term trend: Temperature along 200m contour



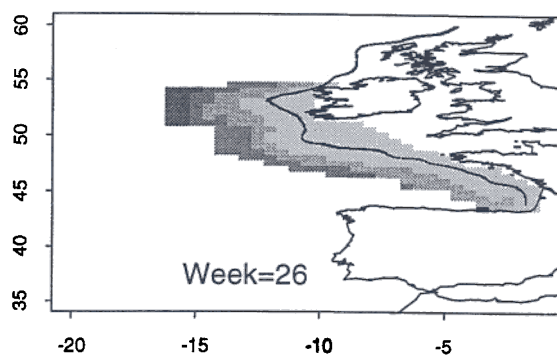


Stage 1 mackerel egg anomalies from long-term (1977-1998) average

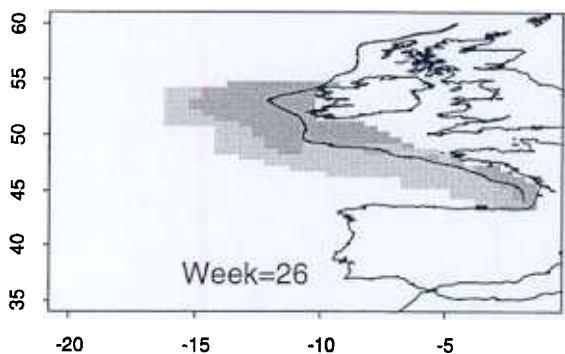
1977



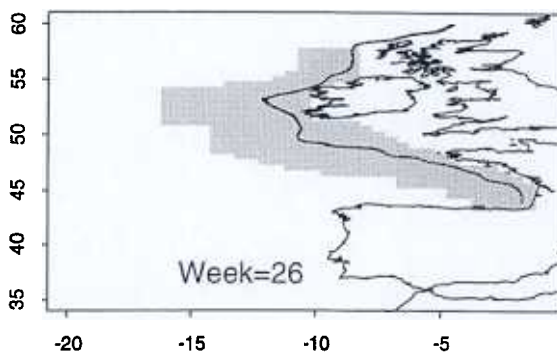
1980



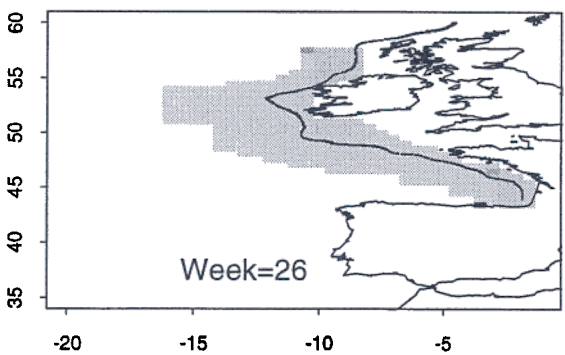
1983



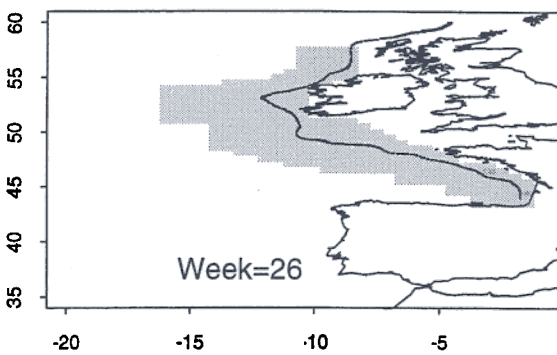
1986



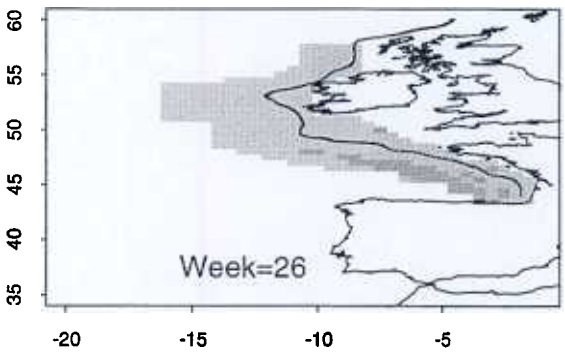
1989



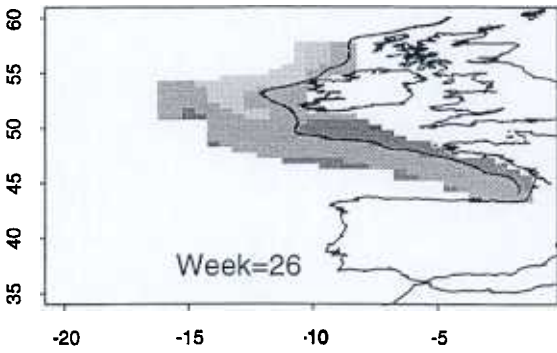
1992



1995



1998



# Stage I Mackerel Eggs along 200m Contour

