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International Council for the
Exploration of the Sea

CM 2000/K:02 Paper
Incorporation of External
Factors in Marine Resource
Surveys

SPATIO-TEMPORAL PATTERNS IN HERRING *(CLUPEA HARENGUS L.)* SCHOOL ABUNDANCE AND SIZE IN THE NW NORTH SEA: MODELLING SPACE TIME DEPENDENCIES TO ALLOW EXAMINATION OF THE IMPACT OF LOCAL SCHOOL ABUNDANCE ON SCHOOL SIZE

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ABSTRACT

As part of the EU funded project CLUSTER a database was constructed of herring schools identified during a series of acoustic surveys in the NW North Sea. Among other descriptors, the database included each schools'; height, length, S_a, and density. The number of schools per 1 nmi EDSU (Elementary Distance Sampling Unit) was also recorded. The relationship between these descriptors and a range of external variables (eg bottom depth, time of day, and location) were examined using a suite of multiple regression models.

The results indicate strong non-linear dependencies on time of day and water depth. Herring school count per EDSU tends to be high during the middle part of the day and lower at dawn and dusk. Furthermore, the 'shape' of this dependence on time of day is non-constant and changes with location. In some areas, for example, herring school count peaks in the morning, and is unimodal; in others it can be bimodal with a peak in the afternoon. Possible explanations for such patterns will be discussed.

Since regression models allow variability due to a mix of explanatory covariates to be assayed and divided, the overall framework can then be used to explore further into the relationships. In this paper we present results showing the density dependent relations among herring schools in the North Sea, ie to what extent does the local school abundance influence the size (energy) of a given school. To achieve this we use the regresson models to remove the effect of time of day, longitude, latitude and bottom depth After this the impact of local school abundance on school size can be ascertained by careful examination of the residuals. The results of this analysis and its implications will be described and discussed.

INTRODUCTION

This work was inspired by the CLUSTER project which is part of the European Community FAIR programme (1997-I 999). The goal of CLUSTER is to characterise schooling behaviour among a range of European pelagic fish species using data collected during acoustic surveys (Reid et al., 2000). Here, we focus on acoustic survey data collected by the Aberdeen Marine Laboratory in the north-west North Sea in July 1991, 1993-1997 (see Fig. 1). The surveys cover the waters surrounding Orkney and Shetland where the most abundant pelagic fish are pre-spawning *Clupea harengus* (Atlantic herring).

The present contribution examines how environmental information (location, time of day and water column depth) influences the numbers of herring schools detected by echo-sounder and how the numbers of fish within each of those schools (back-scattering energy) is simultaneously related to the number of schools recorded in a particular location. We refer to the number of schools in a particular area as the 'density'. Our Null Hypothesis is:

"Small Herring School Size In A Particular Location Is Caused By High Counts Of Nearby Herring Schools."

Addressing this hypothesis is not as trivial as it first appears. It is well established that both counts of herring schools in a particular area and the measurement of each individual school size or acoustic backscattering energy (S,) depend on a host of external factors which can be termed covariables or predictor variables, eg depth or time of day (Swartzman *et al.*, 1995; Swartzmann, 1997; Petitgas and Levenez, 1996). At midday more herring schools are counted, mainly because individual fish and very small groups collect together probably for protection from predators. On the other hand fewer schools are seen at midnight as fish disperse, typically towards the surface to feed (Edwards and Armstrong, 1993). Since interest here centres on a specific effect, viz density-dependence, which is linked to and probably interacts with all the major spatial and temporal effects, it is clear that signal from the important temporal and spatial predictors should be removed before there is any evidence that small or large school size might be caused by high local school count. Another way of seeing this is to consider a specific point in space and time and ask whether the herring schools seen there are either larger or smaller than would be expected given that point in space and time and if so, can any of that extra unexplained variability be attributed to the count (density) of herring schools recorded locally?

Both counts of herring schools and their associated S_a, therefore, depend on multifarious factors and it is clear that statistical procedures should be deployed that allow the removal of such complex trends before the influence of local school count can be quantified.

In this paper we describe one reasonable attempt to find stochastic models for describing average school size and average school count using covariates of location, time of day and bottom depth, confirmed during preliminary analyses as among the most influential variables. Residual variation from each model should then provide information on the dependence of herring school S_a on local school count (density) since variation due to the external factors described above should have been removed.

MATERIALS AND METHODS

Acoustic Surveys and Data

Data for six (1991, 1993-1997) acoustic surveys, all done between mid and late July, were available for the present work (Table 1). The data were collected by FRV Scotia using the Simrad EK500 38-kHz echo-sounder. Data were stored using the BI500 high volume echo data format. The archived BI500 data were then transformed into matrix images in such a manner that each pixel in the image corresponded to a single acoustic back-scattering strength sample from a single echo-sounder transmission.

Information on each school was then extracted using image-processing software (Image-Pro Plus, Media Cybernetics). This procedure combines automated image filtering algorithms with interactive decisions made by the user (Reid and Simmonds, 1993). The threshold for elimination of background scatters was set at -60 dB which provides the optimum effective beam angle for the school volume back-scatter (Sv) of the schools collected. The effective beam angle that samples a school varies with the difference ΔSv between the echo-integration threshold and the true Sv of the school. Herring schools have a volume back-scattering strength in the region of -40 to -45 dB. When ΔSv is in the range (-25<ΔSv>-10 dB) the beam is relatively large but insensitive to variations in the ΔSv. Following thresh-holding a single pass of the morphological filters was used for object preparation. It was found that a -60 dB threshold coupled with the single pass best preserved school morphology and biomass. The objects detected are presented to the user as 'schools' and it is possible to discriminate those of herring from those of other species.

Information is collected almost continually during an acoustic survey as the research vessel steams along its transect path (Fig. 1). In our data, the survey path is divided into 15 minute time intervals termed EDSUs (Elementary Distance Sampling Unit). The herring schools detected by the echo-sounder within each of these compartments are then counted, measured and their biomass determined (Reid et *al.*, 2000). Physical information for each EDSU is also recorded, eg mean depth per EDSU, and mean sea-surface temperature per EDSU, which may be useful in explaining the fish distributions (Reid et *al., 2000).*

Statistical Analyses

Here, we are interested in counts of herring schools recorded per ESDU and the associated back-scattering energy (S,) of each school. School count and school energy (S,) both depend on levels of various other factors in the data (eg depth, longitude, or time of day) and regression models are the most obvious choice for partitioning the signals from each (Bailey et *al.*, 1998; Beare et *al.*, 1998; Daskalov, 1998; Venables and Ripley, 1994; Lindsey, 1995). Discrete count data (numbers of herring schools per EDSU) and continuous data for the school energy (S,) can both be handled within the frameworks of Generalised Linear Models (GLMs) and/or Generalised Additive Models (GAMs) (McCullagh and Nelder. 1989; Hastie and Tibshirani, 1990).

The Poisson distribution is appropriate for count data (Lindsey, 1995) and it was our first choice here for modelling counts of herring schools per EDSU. Application of GLMs and GAMs from the Poisson family to the count data, however, tended to produce over-dispersed models with unacceptably high residual variability (Lindsey, 1995). This large residual variability, caused by clustering of the count data in space and time, makes discrimination between models using conventional Chi-square or Akaike Information Criterion (AIC) tests unreliable. Methods for correcting for over-dispersion in Poisson models are available (see

McCullagh and Nelder, 1983; Lindsey, 1995; Beare and McKenzie, 1999) but were not used here. Instead we opted to account for the higher than expected residual deviances directly by modelling the mean/variance relationship in the data using GLMs and GAMs from the Quasi 'family' (Venables and Ripley, 1994, Lindsey, 1995). Data for school acoustic back-scattering energy (S,) were also modelled with GLMs and GAMs, but this time Gamma error proved to be appropriate since school S_a data are skewed and always positive. Non-linear dependence was described within the GLMs using parametric natural spline functions, and within the GAMs using non-parametric locally-weighted regression smoothers.

RESULTS

Sampling intensity was similar during each of the six surveys (Table 2a), although the numbers of herring schools recorded varied dramatically (Table 2b). In 1997, for example, 1,863 herring schools were seen in 2,239 EDSUs, while in 1995 only 816 schools were seen in 2,052 EDSUs. This information can be translated into a rate of herring school encounter per EDSU (see Table 2b). Mean encounter rates of herring schools in 1995, for example, were half those recorded during the 1996 and 1997 surveys (see Table 2b).

Spatial distributions of the herring school abundance also varied between surveys. In July 1991, most herring were seen north-west of Shetland (see Fig. 1). In 1993 and 1994 highest herring school counts were noted in the Fair Isle current, while more recently (1995, 1996 and 1997) herring were most prevalent to the west of Orkney and Shetland, between the 100 m and 200 m depth contours (Fig. 1).

Generalised Additive Models (GAMs)

As stated, the specific aim of this study is to explore how herring school S_a recorded during six acoustic surveys depends on herring school density, ie the count of schools recorded nearby. To this end the two response variables, counts of herring schools EDSU and the energy (S,) of each school, were modelled using GAMs from the Quasi and Gamma families respectively.

In order to reduce complexity, only longitude, latitude and time of day were considered. The data from each of the six surveys were modelled separately, thereby allowing the spatio-temporal patterns from each to be different. The GAM fits to the count data for 1991 and 1993 surveys are summarised in the analysis of deviance tables (Table 3a, b).

Terms fitted are described in Tables 3a and b using S-plus notation. 'Lo' refers to a locally-weighted regression smoother (Chambers and Hastie, 1991) while 'Lon', 'Lat' and 'Time' are longitude, latitude and time of day respectively. The third and sixth columns show the amount of deviance (variance) reduced following successive introduction of extra terms into the models. The second and fifth columns reflect the 'cost' in degrees of freedom of that reduction in deviance (variance). In the last column we test whether that reduction in deviance is statistically significant given the extra 'cost' in model complexity (degrees of freedom). In the case of the 1991 survey data, the third model is the one chosen because the residual deviance is reduced by 490 from 3,102 to 2,611. To get this 'better' model we actually need 11 less degrees of freedom (see Table **3a).**

The analysis of deviance tests between models 1 and 2 gauges whether time of day explains significant quantities of deviance (variance) when covariables of location are also included; the test between models 2 and 3 ascertains whether the effect of longitude depends on latitude when fime of day is included; while the last test, between models 3 and 4 assays whether the effect of time of day depends simultaneously on longitude and latitude. In other words the last model allows the spatial pattern of herring school occurrence to vary with time of day and tests whether this model is an improvement (statistically) over the one where the spatial pattern is the same at each time of day. For the 1991-1997 surveys, locational covariables, here longitude and latitude, interacted significantly with each other. Time of day, whilst significant as an additive term, was (statistically) independent of both longitude and latitude. This means that for all of the surveys, the shape of the spatial pattern of herring school count per EDSU did not vary with time of day, only the average level changed (Fig. 2).

The equivalent of model 3 (Table 3a), but this time with Gamma error, was chosen to summarise the herring school S_a data. The spatial patterns of average herring school energy are fairly inconsistent between surveys although schools tended to have larger energies around Shetland and in the southern part of the study area in most years. The schools are also larger in the evening. It should be noted here that the average school energy is not necessarily related to total herring biomass. Figure 3 provides **a** summary only of where the largest herring schools are located; not where there are most herring.

GAM-Derived Partial Regressions

Residuals from the two GAM regressions (Figs 2 and 3) are plotted against each other in Figure 4. A linear model was then fitted through the data by least squares. Negative slopes indicate negative density-dependence and vice-versa. According to Figure 4, herring school size/energy (S,) recorded during the '91, '93, '94 and '96 surveys was independent of local school count. In other words, the S_a of any herring school at a particular point in space and time does not depend on the count of schools recorded nearby. In the '95 and '97 surveys, herring school S_a, however, did exhibit some negative density dependence. Some schools had a lower S_a than expected at a specific location, time of day, while others had larger than expected S_a for that location and time of day.

Hexagonal Bins and Generalised Linear Models

The GAM-based analyses of the acoustic data described above reveal interesting patterns, some of which are difficult to explain. Spurious effects may have been caused by non-random sampling, the impact of which can be difficult to assess when using the globally encompassing, GAM-based methods described above. Consequently we opted to investigate the same problem in a different way by sub-setting the data into smaller spatial compartments as opposed to trying to'model dependence on location directly as was done in the GAM-based approach.

To do this, the same data used above were divided into arbitrary spatial compartments using a procedure known as 'Hexagonal Binning' available with S-plus (see Carr et a/., 1987; Carr, 1991; Kaluzny *et* a/., 1997 for details). Locations of sub-regions selected by the procedure are displayed (Fig, 5) and the numbers of observations within each are given in parentheses. Data within each of the 14 sub-regions could then be extracted and modelled as separate subsets of the main data-set. The procedure is intended to lessen the impact of location on our interpretations and allows the more straightforward isolation and assessment of possible sources of bias due to non-random sampling.

In the GAMs described above, longitude, latitude and time of day were used directly as predictor variables and separate models were fitted to the data from each survey (Figs 2 and 3). Here, since the impact of location has been reduced by aggregating the data into 'hexagonal bins' or 'sub-regions', we examine the effect of time of day and bottom depth on the count of herring schools per EDSU and their S_a within each sub-region (Fig. 5). GLMs with Quasi error were appropriate for the counts, and GLMs with Gamma error for the school S_a data. A discrete six-level factor entered the models denoting survey.

The first task was to convince ourselves that the data within each sub-region were actually representative over a sensible range of permutations of bottom depth and time of day for each survey. For instance at noon, in Sub-region 14 during the 1991 survey, there should be observations reasonably evenly spread along the entire depth range within the area. Similarly at 100 m in 1993 in Sub-region 10, sampling must have been done at regular intervals throughout the day. These important aspects are more transparent and easier to interpret when smaller subsets of the data are examined (Beare and McKenzie, 1999).

The results of the analyses on the individual hexagonal sub-regions of >300 observations are described below. The model selection procedure was guided, in addition to statistical considerations, by our biological knowledge of the data. The dependence of herring counts and school S_a on time of day and bottom depth was unlikely to be linear (Figs 2, 3 and 4) and so, after experimentation, both the discrete count data and the continuous school S_a data were fitted to the time of day, depth and survey variables using parametric natural spline functions.

'Best' models were selected using a painstaking, manual approach. This was favoured over automated procedures which may often obscure difficulties associated with non-random sampling (Beare and McKenzie, 1999a, b, c). The use of natural spline functions to model non-linearity involves the selection of a degrees of freedom parameter. This quantity is reflected in the flexibility of the curve fitted. Separate models fitted to each covariate separately (time of day, bottom depth and year) initially provided useful guides as to reasonable numbers of degrees of freedom needed in the spline function and hence the shape needed for each covariate. Once such shapes were established, all of the covariates were combined in a single multiple regression model. Further diagnostic checks were then done, and the importance of each covariate, given the presence of others in the model, was assayed statistically. Lastly, standard model checking and residual analyses were done (Chambers and Hastie, 1992) and the significance of the fit to the data was ascertained using Chi-square tests (see Beare and McKenzie, 1999a, b, c).

Interaction terms between the three covariates (time of day, bottom depth and year/survey) were not included, although there is evidence that some may well be statistically 'significant'. This option was taken for a variety of reasons. Firstly, it drastically simplifies the model-selection problem, and secondly all the GLMs selected with covariates as independent terms "fitted" the data adequately. It should also be noted that interactions are actually allowed to occur within our overall data-analytic framework (both GLM and GAM) via the separate modelling of the data in smaller subsets. The shapes of time of day and/or depth dependencies, for example, can and do vary between surveys (Figs 2 and 3) and between sub-regions (Figs 6, 7, 8 and 9) and the global perception by the investigator is that interactions are occurring throughout the analysis; although not formally fitted within the models (GLM).

Our opinion is that the 'simple' GLM summaries we obtained by modelling the terms independently are useful descriptions of the data which provide novel insights into schooling behaviour of herring. Further, since the models fit they are useful for removing signals due to bottom depth and time of day they allow the sole impact of school count per EDSU on school S_a to be examined with a satisfactory level of confidence.

Sub-Region 2

Sub-region 2 is located to the south-west of Orkney. During the six surveys, a total of 422 observations were made. The maximum number of herring schools seen within an EDSU was eight during the July 1994 survey. Sea surface temperature and salinity ranges are given in Table 4a. The bottom depth and temporal (hourly) ranges of sampling spanned in sub-region 2 during each survey also varied. In 1995, for example, observations were only available from 0206 to 0430 GMT at depths of between 79 m and 84 m.

During all surveys the majority (335) of the EDSUs covered had zero school counts. Of the EDSUs where herring schools were counted, school S_a varied between a minimum of 2.6 via a median of 23.7 to a maximum of 2,081.

Only data from the 1991, 1994 and 1996 surveys were used in the GLMs. Time of day was significant and its dependence was summarised using a natural spline function (de Boor, 1978) with 4 degrees of freedom (df) (see Fig. 6). The effect of bottom depth was significant, non-linear and also required 4 df (Table 5). The diel pattern of herring school abundance was weakly bimodal with peaks at ca 0700 GMT and ca 1500 GMT but these conclusions should be treated cautiously due to data-sparsity (Fig. 6).

The output from the model also permits dependence due to bottom depth within each sub-region, given a particular time of day, to be examined. Identical data matrices used in plotting Figure 6 were thus transposed to produce Figure 7 which allows dependence on bottom depth, given a particular time of day to be visualised. Numbers of herring schools seen increases with bottom depth in Sub-region 2 and it can also be noted here that the magnitude of variability due to time of day is comparatively small (Fig. 7).

GLMs from the Gamma family were used to summarise the dependence of school S_a on the time of day, bottom depth and year covariates. In Sub-region 2, 4df were selected for time of day while bottom depth, given the inclusion of time of day, failed to explain significant quantities of the variability (Table 6; Figs 8 and 9). School S_a was high in the morning and evening, although there was an odd peak at ca 1100 which may be due to a sampling inconsistency. The indirect relationship between the average herring school count and their S_a is clear (compare Figs 6 and 8).

Sub-Region 3

The 1993 and 1995 surveys were omitted from the analysis due to data sparsity. Sampling done is summarised in Table 4b. Time of day, depth and year all explained statistically significant amounts of variability in the school counts. Time of day required a spline function with 5 df (Table 5), depth 3 df and year entered the model as a four-level factor.

Peak numbers of herring schools were seen at ca 0900 GMT (Fig. 6) after when average counts fell, although there was a small ‘shoulder’ at ca 1500 GMT. Mean herring school counts declined as bottom depths increased between 90 m and 150 m and the rate of decline increased after 125 m.

Average school S_a also depended on time of day, bottom depth and survey. Five df were used for time of day, while bottom depth was found to be linear (Table 6). The shapes of these dependencies are displayed in Figures 8 and 9. Herring school S_a exhibited broadly opposite behaviour to the counts (Figs 6 and 7) decreasing gradually with bottom depth. Herring schools had the highest average S_a in the morning, after which time S_a decreased and a minimum was recorded at ca 1400 GMT (Figs 8 and 9).

Sub-Region 5

Sub-region 5 is situated west of Orkney (Fig. 3). 1,103 observations were made in the area during the six surveys. Visual examinations suggested that sampling coverage was adequate along both time of day and bottom depth trajectories (see Table 4c). Maximum average counts of herring schools per EDSU were seen in the morning at ca 0800 GMT, while the counts increased steadily with bottom depth (see Figs 6 and 7). Average school S_a in Sub-region 5 was also modelled successfully using time of day and bottom depth predictors (Table 6, Figs 8 and 9). According to the data, herring schools had minimum mean S_a at ca 1000 GMT, at bottom depths of ca 125 m (Figs 8 and 9).

Sub-Region 6

This region is situated in the Fair Isle current, east of Orkney. Mean herring school count increased as the day progressed and fell as it ended, (Fig. 6) but there was no obvious peak. Numbers of herring schools increased gradually with depth to peak at ca 115 m (Fig. 7) after which they again decreased. Average herring school S_a was lowest at *ca* 125 m (Fig. 9) and highest in the evening (Fig. 8).

Sub-Region 7

Sub-region 7 is located on the south-eastern periphery of the study region and was relatively well sampled, although herring schools themselves were rare in the area. Average bottom depths ranged from 97 m to 157 m. **Sea** surface temperatures and salinities, during the six July surveys, spanned the range 11.5-15.3°C and 33.1-35.2‰ (Table 4e) respectively. Mean counts of herring schools had a unimodal shape over the course of an average **day,** the peak occurring at 1200 GMT (Fig. 4). School counts declined linearly (on the scale of the predictor) with increasing depths (Fig. 5). Average school S_a was highest in the evening and lowest at a depth of *ca* 130 m (Figs 7 and 8).

Sub-Region 10

Sampling effort was particularly high in Sub-region 10, situated west of Shetland, (Fig. 5) where 2,577 observations were made altogether during the six surveys. The dependence of herring school counts on time of day was bimodal in shape (Table 5). The first peak of the day occurred in the morning at ca 0800 GMT while the second, smaller peak appeared later in the day at ca 1800 GMT (Fig. 6). A unimodal function with a maximum at ca 130 m described the relationship between herring school count and bottom depth (3 df. Table 5). Individual mean school energies were highest in the morning and mid afternoon (Fig. 6) and lowest at ca 130 m.

Sub-Region 11

This region is located west of Shetland. High counts of herring schools were recorded in the area during the 1991, 1996 and 1997 surveys (Fig. 2). During the day there were two peaks of herring school count (Fig: 6), the first smaller peak was recorded at ca 0800 GMT, and the second larger peak at ca 1600 GMT. Mean school count increased steadily with rising depth, peaking at ca 140 m (Fig. 7).

Sub-Region 12

Four hundred and eighty seven observations were made in Sub-region 12 during the six surveys. 1991 and 1994 data were discarded because of inadequate sampling coverage (Table 4h). Dependence of school count on time of day was weakly bimodal in shape with a maximum occurring particularly early in the morning at ca 0630 GMT followed by a much smaller evening peak at ca 2000 GMT. Numbers recorded decreased steadily between depths of 90-160 m. Herring school S_a peaked at noon while the shape of the depth dependence was similar to that described in the other sub-regions with minimum S_a schools recorded at depths of ca 125 m.

Sub-Region 14

This area is directly north of Shetland and is characterised by steep depth gradients, relatively deep, warm, salty Atlantic water (Table 4g) and high numbers of herring. Extensive sampling was done during ail surveys (Table 4g), although there were no data collected after 2015 GMT in 1994, and none deeper than 209 m in 1997. Numbers of herring schools exhibited a strongly bimodal dependency against time of day with sharp maxima at ca 0830 GMT and ca 1800 GMT (Fig. 6; Table 5). The second peak in the day was only slightly larger than the first. As far as bottom depth is concerned, herring school count increased steadily moving into deeper water and peaked at *ca 140* m, (Fig. 7). School S_a was high at mid-day and early evening (Fig. 8) and declined steadily with bottom depth (Fig. 9).

Sub-Region 15

Sub-region 15 is west of Shetland and has the highest average depth (Fig. 5; Table 4h) in the study region. Over the daily cycle, average herring school count was weakly bimodal in shape with maxima at ca 0830 GMT and ca 1430 GMT (Fig. 6). The second peak in the day was larger than the first and was similar to the patterns observed in Sub-regions 11 and 12. School counts increased with depth, the shape of the function being similar to those of Sub-regions 10, 11, and 14. The final model selected for the count data had 5 df for time of day and 3 df for bottom depth (Table 5). Average school S_a was lowest in the morning and evening, peaked at ca 1400 GMT, and decreased steadily with increasing bottom depth (Figs 8 and 9).

GLM-Derived Partial Regressions

The residuals from the GLMs (Quasi) for counts are plotted against the residuals from the GLMs (Gamma) for the school S_a for each Sub-region in Figure 10. In Sub-regions 2, 3, 6, 7, 12, 14, and 15 there is no statistically significant slope of either sign and therefore no dependency between the S_a of each school and the local count that cannot be explained by dividing the data into spatial subsets and modelling the variation left in the data as **a** function of time of day and bottom depth. Significant negative slopes, however, were found in the south-western portion of the study region, in Sub-regions 5, 10 and 11.

DISCUSSION

The two complimentary partial regression approaches described may seem unnecessarily laborious. It must, however, be remembered that we are aiming to extract an extremely subtle signal from data exhibiting complex non-linear and multivariate dependencies. Only by attempting the very difficult removal of signals due to the local environment (eg bottom depth and time of day), can we have confidence that residual variability left unexplained is due to any specific factor, eg the number of local herring schools.

It is well known (Figs 2, 3, 6, 7, 8 and 9) that numbers of fish schools counted on acoustic surveys tend to increase as the day progresses, and that the energy (S,) of each school simultaneously decreases (Edwards and Armstrong, 1983; MacLennan, 1990; Petitgas and Levenez, 1996; Swartzman, 1997). This reduction in school S_a, though, may not necessarily be caused by high counts of schools nearby. Average school count increases and their respective S_a falls due to the diurnal behaviour of the fish which is connected with feeding and predator avoidance (Olsen, 1990). Similarly more, smaller herring schools are seen at bottom depths between 115 m and 140 m but they or may not actually be smaller or have lower energies because they have more neighbours.

Our partial regression approach allows us to assign variability in herring school S_a specifically to the number of schools recorded locally and the results described in this study suggest that herring school S_a is most often independent of local school count. This means that herring school S_a at a specific point in space and time conveys little information about how many schools are nearby and similarly, local school count per EDSU provides little information as to the size of herring school to be expected.

In some instances, however, negative density-dependence was indeed detected in the herring data. The energy (S,) of some herring schools does seem to be influenced by local school count after making allowances for the spatial and temporal effects. It follows that some herring schools have higher/lower average energies (Sa) than would be expected from a simple consideration of location, time of day and bottom depth, and that some of the extra variation in school S_a data may be explained by reference to local school count.

Two different modelling approaches were adopted in this paper to address the same problem. In the first, GAMs were used to model the dependence of the school counts and energies on three predictor variables (longitude, latitude and time of day) for each year separately (see Figs 2 and 3) while in the second, GLMs were used to model the dependence of the school counts and energies on time of day, depth and year within separate spatial compartments.

The GAM-based approach suggests weak density-dependence of herring school S_a occurred during the 1995 and 1997 surveys, while the GLM-based approach suggests weak density-dependence within Sub-regions 5, 10 and 11. It is certainly possible that the negative density dependencies that we identified are artefacts of inadequate trend removal.

If, however, we consider them to be genuine effects it implies that school energy falls as school count increases, faster than would be expected for that particular location depth and time of day. Negative density dependence was detected by the GAM-based approach in the 1995 and 1997 survey data when the majority of herring biomass was situated west of the Orkney-Shetland Ridge in relatively warm, saline Atlantic water; and by the GLM-based approach in three sub-regions also to the west of the Orkney-Shetland Plateau It is likely that some aspect of the behaviour of herring in two areas west and east of the Orkney-Shetland Plateau is different.

Returning to our original Null Hypothesis it appears that the herring schools west of the Orkney-Shetland Plateau are smaller (have lower energies) when there are high counts of nearby schools. It means that some of the fish detected acoustically in the larger schools are not detected in the smaller, more numerous schools, causing lower school energies to be measured than would be expected at that point in space and time. These 'lost' fish might be swimming singly; or be in much smaller groups, not identified as schools by the rather arbitrary criterion of an 'acoustic school' that we used (see Kieser et *al.*, 1993 and Reid et *al.*, 2000). In summary there do appear to be regional differences in the aggregative behaviour of herring which may be due to regional differences in migration activity, spawning or age structure. Clearly these aspects require further investigation.

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TABLE 1

Timing of July acoustic surveys between 1991 and 1997

Survey	Start date (July)	End date (July)
1991	13	31
1993	11	29
1994	7	25
1995	9	26
1996	14	30
1997	9	27

TABLE 2A

Numbers of observations made during each acoustic survey

Survey	1991	1993	1994	1995	1996	1997
N	2,221	2,234	2,364	2,052	2,140	2,239

TABLE 2B

Numbers of herring schools observed during each acoustic survey

Survey	1991	1993	1994	1995	1996	1997
Schools	1,672	1,423	1,388	816	1,792	1,863
Schools/n	0.7528	0.6370	0.5871	0.3977	0.8374	0.8321

TABLE 3A

Results of Generalised Additive Model fits to herring count data for 1991. (NB smoothing span = 0.06)

Terms	Resid Df	Resid Dev	Test	Df	Dev	Pr (F)
1. Lo (Lon) + lo (Lat)	2,149	3,940				
2. Lo (Lon) + lo (Lat) + lo (Time)	2,119	3,102	+ lo (Time)	30.7	838	<0.01
3. Lo (Lon, Lat) + lo (Time)	2,130	2,611	2 vs 3	-11	490	<0.01
4. Lo (Lon, Lat, Time)	2,147	3,276	3 vs 4	-17	-664	<0.01

TABLE 3B

Results of Generalised Additive Model fits to herring count data for 1993. (NB smoothing span = 0.06)

Terms	Resid Df	Resid Dev	Test	Df	Dev	Pr (Chi)
1. Lo (Lon) + lo (Lat)	2,159	3,584				
2. Lo (Lon) + lo (Lat) + lo (Time)	2,128	3,164	+ lo (Time)	31	420	<0.01
3. Lo (Lon, Lat) + lo (Time)	2,147	2,874	2 vs 3	-19	290	<0.01
4. Lo (Lon, Lat, Time)	2,163	3,389	3 vs 4	-16	-515	<0.15

TABLE 4A

Data ranges in Sub-region 2

	n	Time (GMT)	SST (°C)	SSS (‰)	Depth (m)
1991	121	2.2-16.9	NA	NA	44.6-116.6
1993	45	5.7-11.8	NA	NA	36.9-93.3
1994	145	2.1-22.0	10.6-12.9	34.3-34.6	42.4-126.7
1995	20	2.6-4.5	10.6-11.7	34.6-34.8	64.1-79.5
1996	71	6.6-19.6	10.8-11.5	34.6-34.9	60.2-117.6
1997	20	5.5-11.4	12.1-13.2	34.9-35.1	63.0-78.1

TABLE 4B

Ranges of covariables in Sub-region 3

	n	Time (GMT)	SST (°C)	SSS (‰)	Depth (m)
1991	171	2.1-22.0	NA	NA	88.8-151.6
1993	29	14.4-18.7	NA	NA	110.5-146.3
1994	199	2.1-21.8	12.2-15.1	34.4-34.9	82.1-153.6
1995	27	8.4-11.1	11.9-12.8	35.0-35.1	106.1-149.6
1996	104	2.4-22	11.5-12.6	34.8-35.1	91.7-164.2
1997	73	4.8-21.9	12.7-13.8	35.1-35.2	103.8-153.4

TABLE 4C

Ranges of covariables in Sub-region 5

	n	Time (GMT)	SST (°C)	SSS (‰)	Depth (m)
1991	179	2.2-21.5	NA	NA	40.6-156.9
1993	181	2.1-22.0	NA	NA	37.4-192.4
1994	183	2.1-20.5	11.2-13.5	34.0-35.1	35.4-154.9
1995	170	2.0-21.9	11.2-13.8	33.2-35.0	40.1-183.9
1996	181	3.8-20.7	11.2-12.9	34.5-35.2	51.9-175.6
1997	212	2.0-21.9	11.0-14.5	34.9-35.2	48.8-199.8

TABLE 4D

Ranges of covariables in Sub-region 6

	n	Time (GMT)	SST (°C)	SSS (‰)	Depth (m)
1991	284	2.2-22	NA	NA	36.9-149.9
1993	358	2.1-22	NA	NA	38.6-157.6
1994	319	2.1-22	10.8-13.2	34.1-35.1	45.2-147.2
1995	322	2.0-22	10.4-13.3	34.5-35.2	36.4-159.8
1996	331	1.9-22	10.7-12.5	34.6-35.2	32.8-157.3
1997	321	2.1-22	10.5-13.3	35.1-35.3	34.5-157.2

TABLE 4E

Ranges of covariables in Sub-region 7

	N	July Date		Time (GMT)		SST		SSS		Depth (m)	
1991	126	15	18	6.5	22.0	NA	NA	NA	NA	113.1	154.4
1993	323	11	16	2.1	21.7	NA	NA	NA	NA	97.4	149.4
1994	198	9	12	2.2	20.2	12.0	14.4	34.2	35.1	107.4	152.2
1995	285	9	13	2.1	22.0	12.8	15.3	33.1	35.2	100.5	154.0
1996	188	14	18	2.1	22.0	11.5	12.6	34.8	35.1	101.1	156.6
1997	187	10	14	2.0	21.9	12.9	14.6	34.7	35.2	102.7	152.8

TABLE 4F

Ranges of covariables in Sub-region 10

	N	Time (GMT)	SST (°C)	SSS (‰)	Depth (m)
1991	360	2.0-21.9	NA	NA	52.4-247.9
1993	364	2.1-22.0	NA	NA	51.5-244.7
1994	424	2.1-22.0	10.7-13.5	34.3-35.1	52.0-243.6
1995	336	2.0-21.9	10.9-12.7	35.1-35.3	52.2-240.4
1996	471	2.0-21.9	10.7-12.7	34.5-35.3	51.8-245.6
1997	425	2.0-21.9	11.1-14.3	35.1-35.4	52.5-214.9

TABLE 4G

Ranges of covariables in Sub-region 11

	n	Time (GMT)	SST (°C)	SSS (‰)	Depth (m)
1991	326	2.1-22	NA	NA	62.7-163.1
1993	296	2.1-22	NA	NA	63.3-166.1
1994	352	2.0-22	11.6-13.8	35.0-35.2	59.9-170.2
1995	401	2.1-22	10.3-14.5	34.6-35.3	58.0-166.4
1996	366	2.3-22	10.8-12.8	34.3-35.3	62.3-163.3
1997	438	2.1-22	11.3-14.0	34.8-35.3	59.1-166.0

TABLE 4H

Ranges of covariables in Sub-region 12

	n	Time (GMT)	SST (°C)	SSS (‰)	Depth (m)
1991	30	18.2-19.7	NA	NA	124.5-150.7
1993	165	2.0-22.4	NA	NA	92.5-160.4
1994	26	12.9-18.0	12.7-13.2	35.1-35.1	120.9-153.6
1995	125	7.0-18.6	13.4-14.8	33.2-35.1	94.0-159.0
1996	28	2.1-22.0	11.9-12.0	34.7-35.2	122.8-151.1
1997	113	2.0-22.0	13.6-14.9	33.5-35.2	111.1-153.7

TABLE 4G

Ranges of covariables in Sub-region 14

	N	Time (GMT)	SST (°C)	SSS (‰)		Depth (m)	
1991	130	2.1-21.9	NA	NA	NA	95.0-	239.2
1993	108	2.0-21.9	NA	NA	NA	91.1-	241.4
1994	196	2.6-20.3	11.4-13.4	34.9-	35.2	89.5-	247.6
1995	182	2.0-21.9	11.4-13.0	35.1-	35.3	86.0-	248.9
1996	174	2.0-21.9	11.6-12.6	34.5-	35.3	87.0-	247.5
1997	153	2.0-21.9	12.0-14.0	35.3-	35.4	93.2-	209.3

TABLE 4H

Ranges of covariables in Sub-region 15

	N	Day		Time		SST		SSS		Depth		nschools	
1991	204	20	25	3.5	20.3	NA	NA	NA	NA	123.4	248.5	0	12
1993	191	20	22	3.0	21.5	NA	NA	NA	NA	121.2	247.7	0	4
1994	198	15	19	2.0	22.0	12.9	13.6	35.0	35.2	116.2	242.2	0	9
1995	141	16	20	2.0	22.0	12.1	13.2	35.1	35.2	118.5	211.5	0	2
1996	131	21	23	2.0	21.9	11.9	12.3	35.1	35.3	117.2	185.2	0	8
1997	246	17	21	2.0	21.9	12.9	14.8	34.0	35.3	115.0	207.1	0	10

TABLE 5

Summary of best GLM (Quasi) fitted to the herring school count data. DF refers to the number of degrees of freedom selected in the natural spline smoothing function

Sub-region	Time	Depth	Year
2	4 df	4 df	Factor
3	5 df	3 df	Factor
5	4 df	2 df	Factor
6	5df	5 df	Factor
7	6 df	Linear	Factor
10	6 df	3 df	Factor
11	5 df	2 df	Factor
12	6 df	2 df	Factor
14	4 df	3 df	Factor
15	5 df	3 df	Factor

TABLE 6

Summary of best GLMs (Gamma) fitted to the herring school energy data. DF refers to the number of degrees of freedom selected in the natural spline smoothing function

Sub-region	Time	Depth	Year
2	4 df	Non sig	Factor
3	5 df	Linear	Factor
5	3 df	2 df	Factor
6	4 df	2 df	Factor
7	4 df	2 df	Factor
10	3 df	2 df	Factor
11	4 df	2 df	Factor
12	4 df	2 df	Factor
14	5 df	3 df	Factor
15	6 df	2 df	Factor

FIGURE LEGENDS

Figure 1. Acoustic surveys between 1991 and 1997. Circles represent numbers of herring schools recorded.

Figure 2. Spatial and diel pattern in herring school numbers recorded in the survey area in July 1991, 1993-1997.

Figure 3. Diel pattern in mean herring school S_a in the survey area in July 1991, 1993-1997.

Figure 4. Density dependence in the Herring Schools. 1995 and 1997 surveys have statistically significant (negative) slopes.

Figure 5. Location of hexagonal bins. Numbers of observations (1991, 1993-1997) are in parentheses.

Figure 5. Diel dependence of average herring school count at 10 different bottom depths (for location of sub-regions see Fig. 5) during the 1994 survey.

Figure 6. Depth dependence of herring school counts at 10 different times of day during the 1994 survey.

Figure 7. Diel dependence of mean herring school S_a on Time of day during the 1994 survey at 10 different Bottom depths.

Figure 8. Dependence of Herring school energy on Bottom depth during the 1994 survey at 10 different Times of Day.

Figure 9. Density dependence among the 10 Bins.

Figure 1

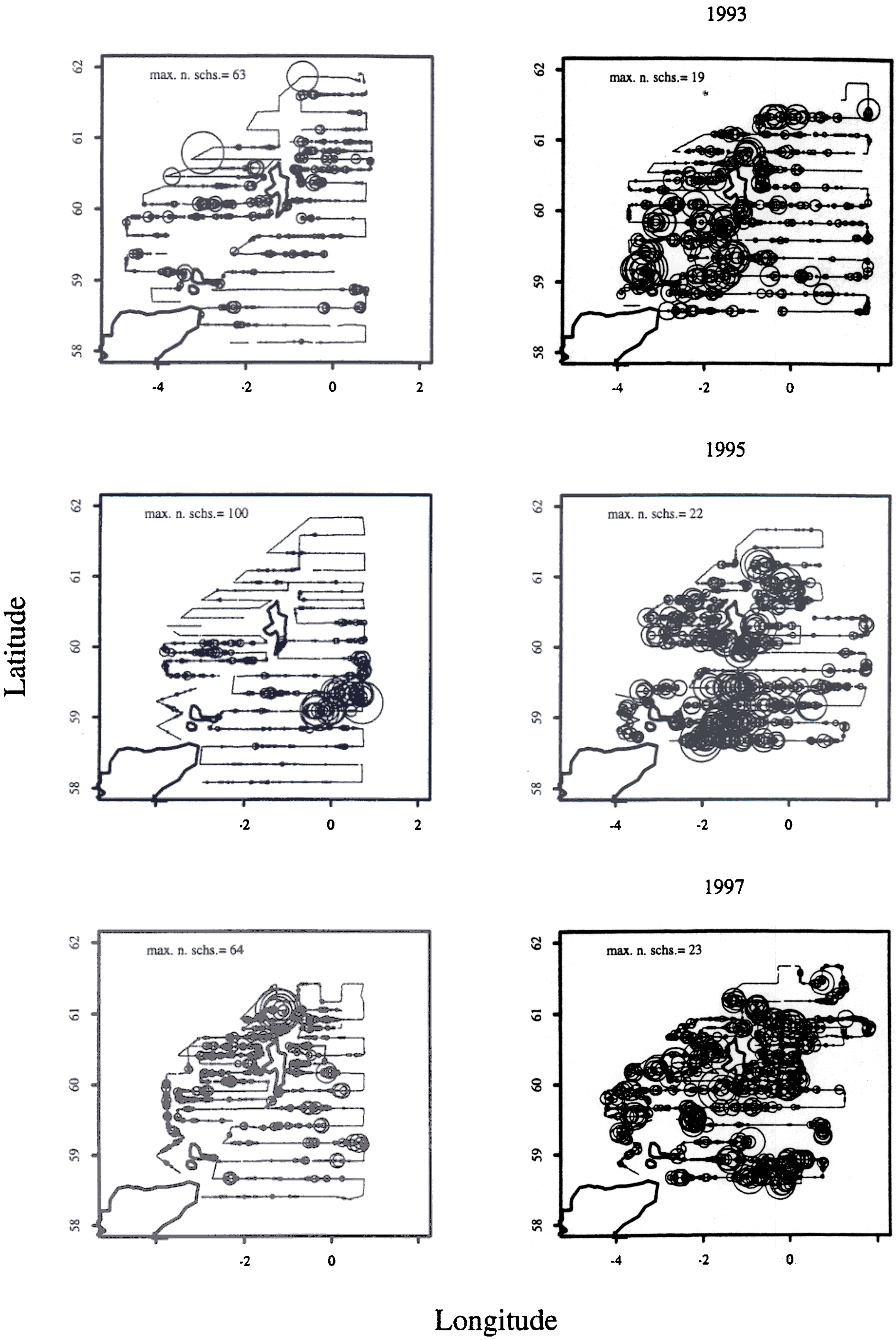
1993
max. n. schs.= 63
max. n. schs.= 19
1995
max. n. schs.= 100
max. n. schs.= 22
1997
max. n. schs.= 64
max. n. schs.= 23
Latitude
Longitude
62
61
60
59
58
-4
-2
0
2

Figure 2


91 @ 400 GMT
91 @ 700 GMT
91 @ 1100 GMT
91 @ 1400 GMT
91 @ 1800 GMT
91 @ 2100 GMT
93 @ 400 GMT
93 @ 700 GMT
93 @ 1100 GMT
93 @ 1400 GMT
93 @ 1800 GMT
93 @ 2100 GMT
94 @ 400 GMT
94 @ 700 GMT
94 @ 1100 GMT
94 @ 1400 GMT
94 @ 1800 GMT
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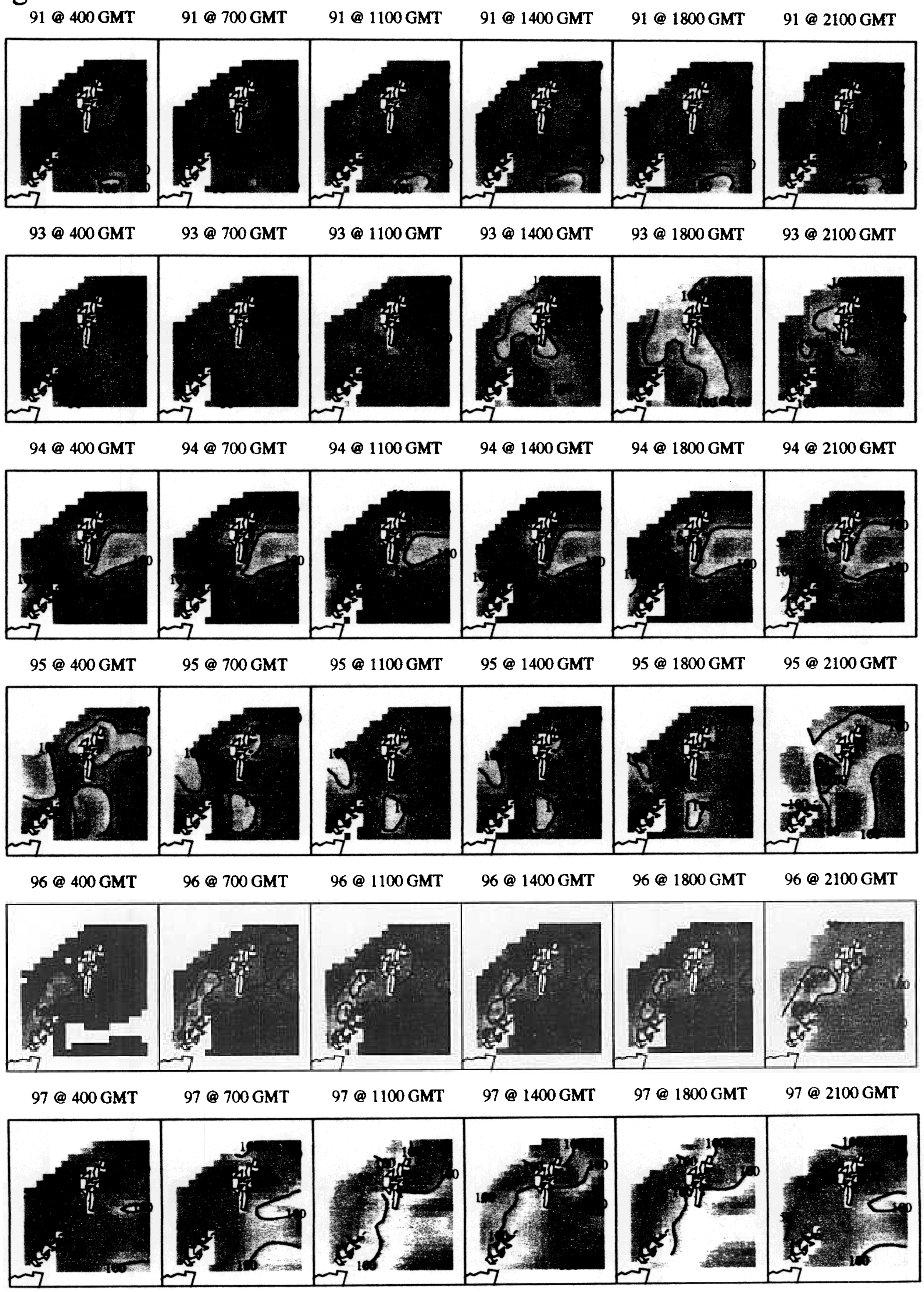
96 @ 400 GMT
96 @ 700 GMT
96 @ 1100 GMT
96 @ 1400 GMT
96 @ 1800 GMT
96 @ 2100 GMT
97 @ 400 GMT
97 @ 700 GMT
97 @ 1100 GMT
97 @ 1400 GMT
97 @ 1800 GMT
97 @ 2100 GMT

Figure 3


91 @ 400 GMT
91 @ 700 GMT
91 @ 1100 GMT
91 @ 1400 GMT
91 @ 1800 GMT
91 @ 2100 GMT
93 @ 400 GMT
93 @ 700 GMT
93 @ 1100 GMT
93 @ 1400 GMT
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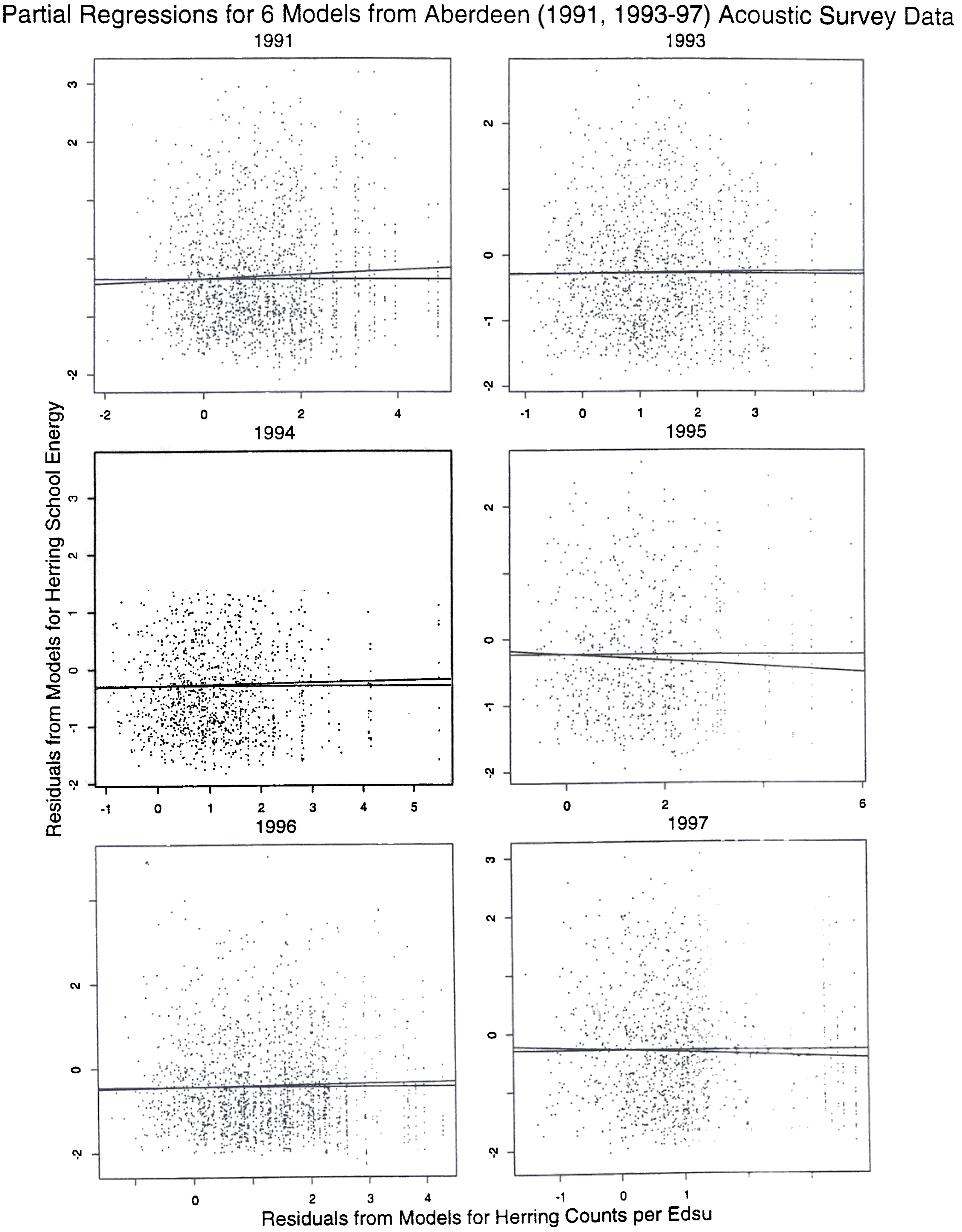
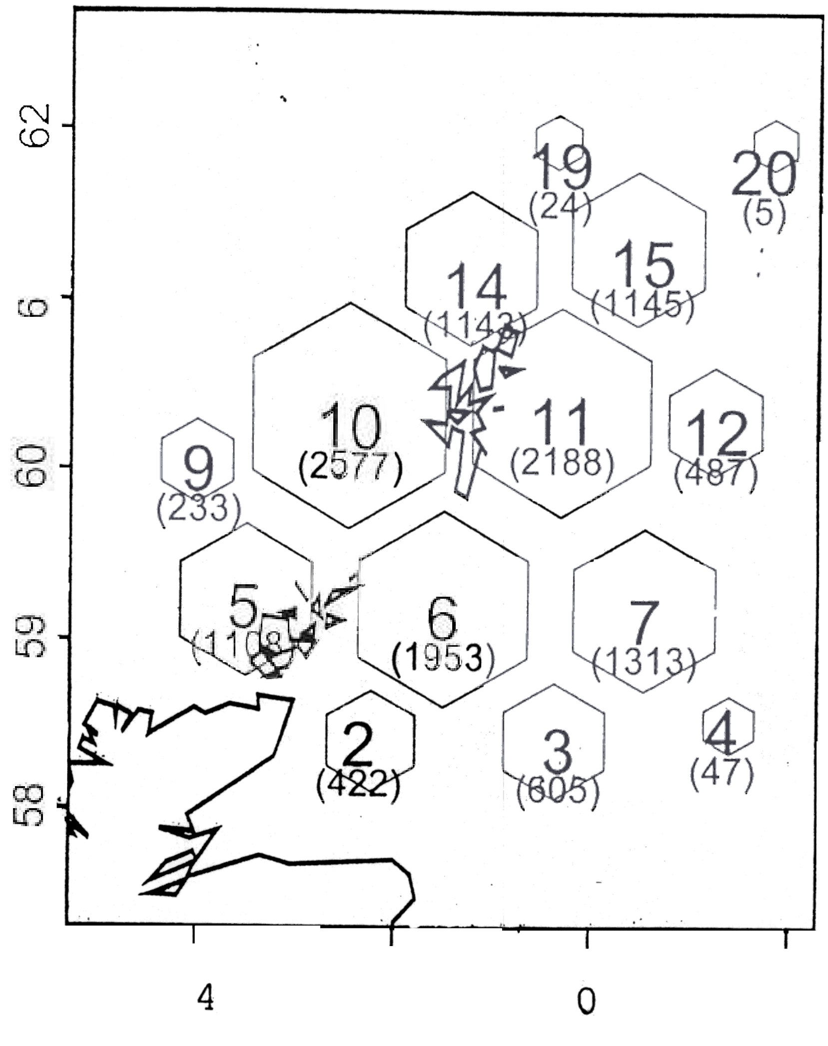
97 @ 1400 GMT
97 @ 1800 GMT
97 @ 2100 GMT

Figure 4


Partial Regressions for 6 Models from Aberdeen (1991, 1993-97) Acoustic Survey Data
1991
1993
1994
1995
1996
1997
Residuals from Models for Herring School Energy
Residuals from Models for Herring Counts per Edsu



62
6
60
59
58
4
0
19
(24)
20
(5)
14
(1143)
15
(1145)
10
(2577)
11
(2188)
12
(487)
9
(233)
5
(1108)
6
(1953)
7
(1313)
2
(422)
3
(605)
4
(47)

Figure 6

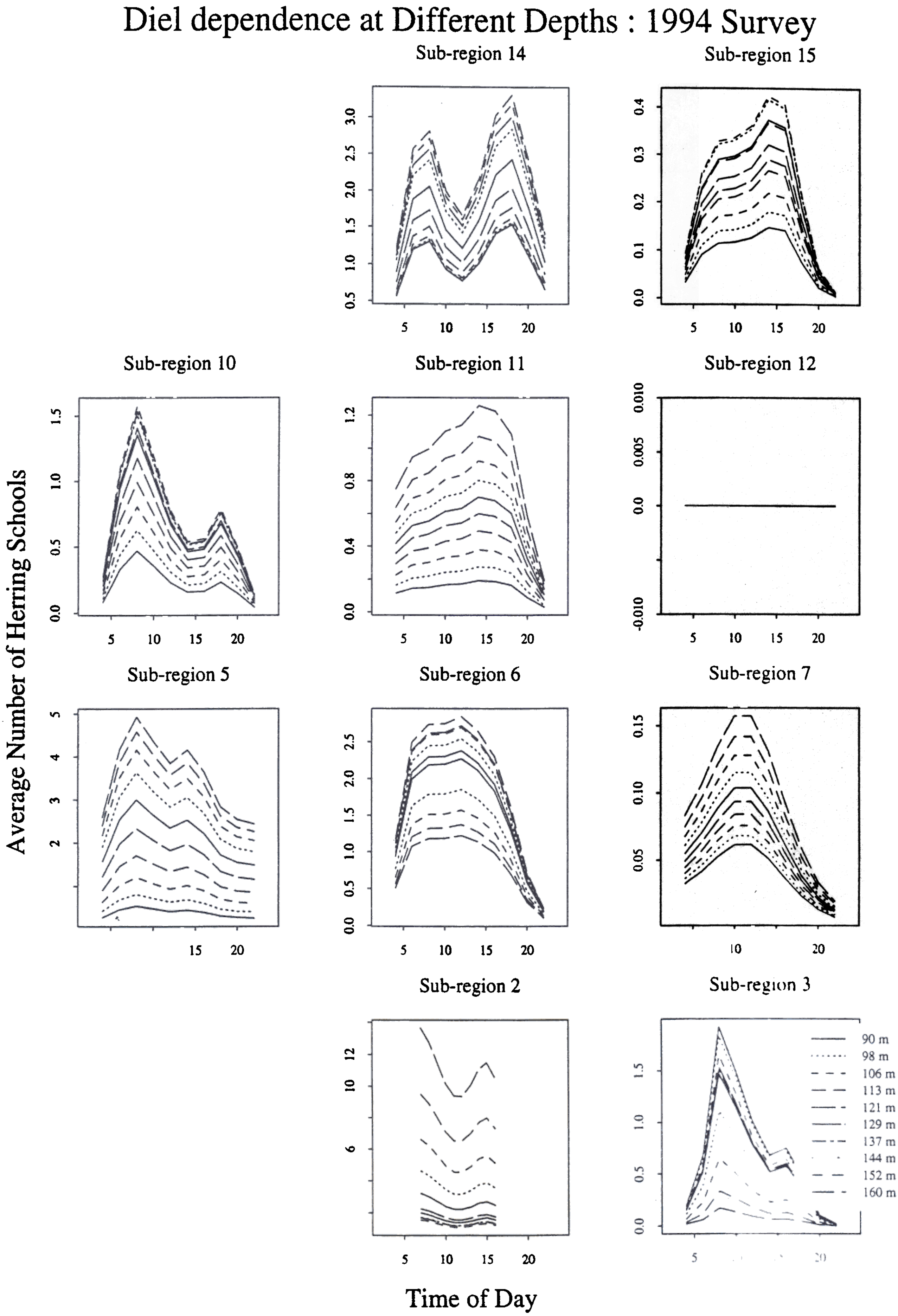

Diel dependence at Different Depths : 1994 Survey
Sub-region 14
Sub-region 15
Sub-region 10
Sub-region 11
Sub-region 12
Sub-region 5
Sub-region 6
Sub-region 7
Sub-region 2
Sub-region 3
Average Number of Herring Schools
Time of Day
90 m
98 m
106 m
113 m
121 m
129 m
137 m
144 m
152 m
160 m

Figure 7

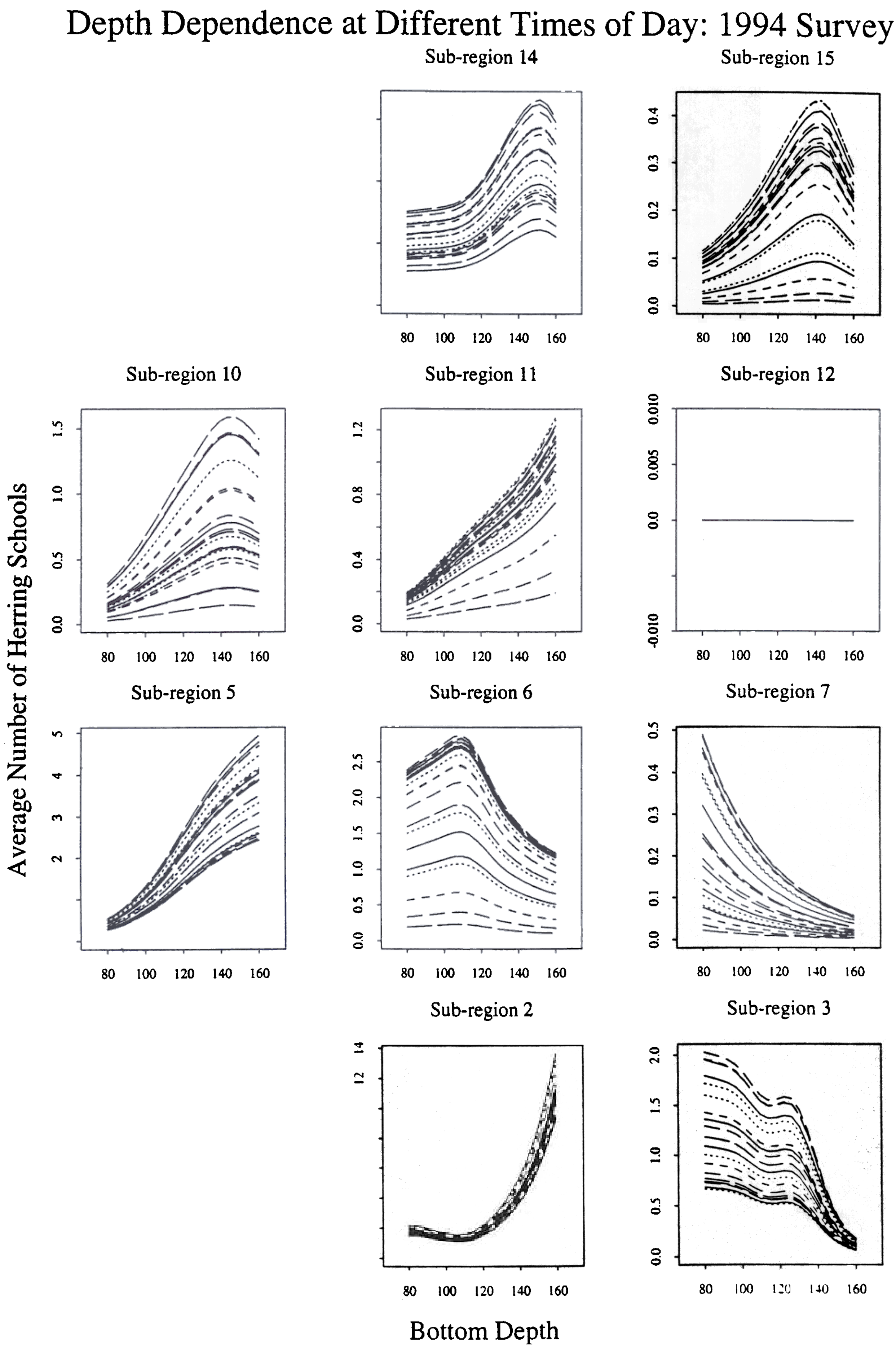
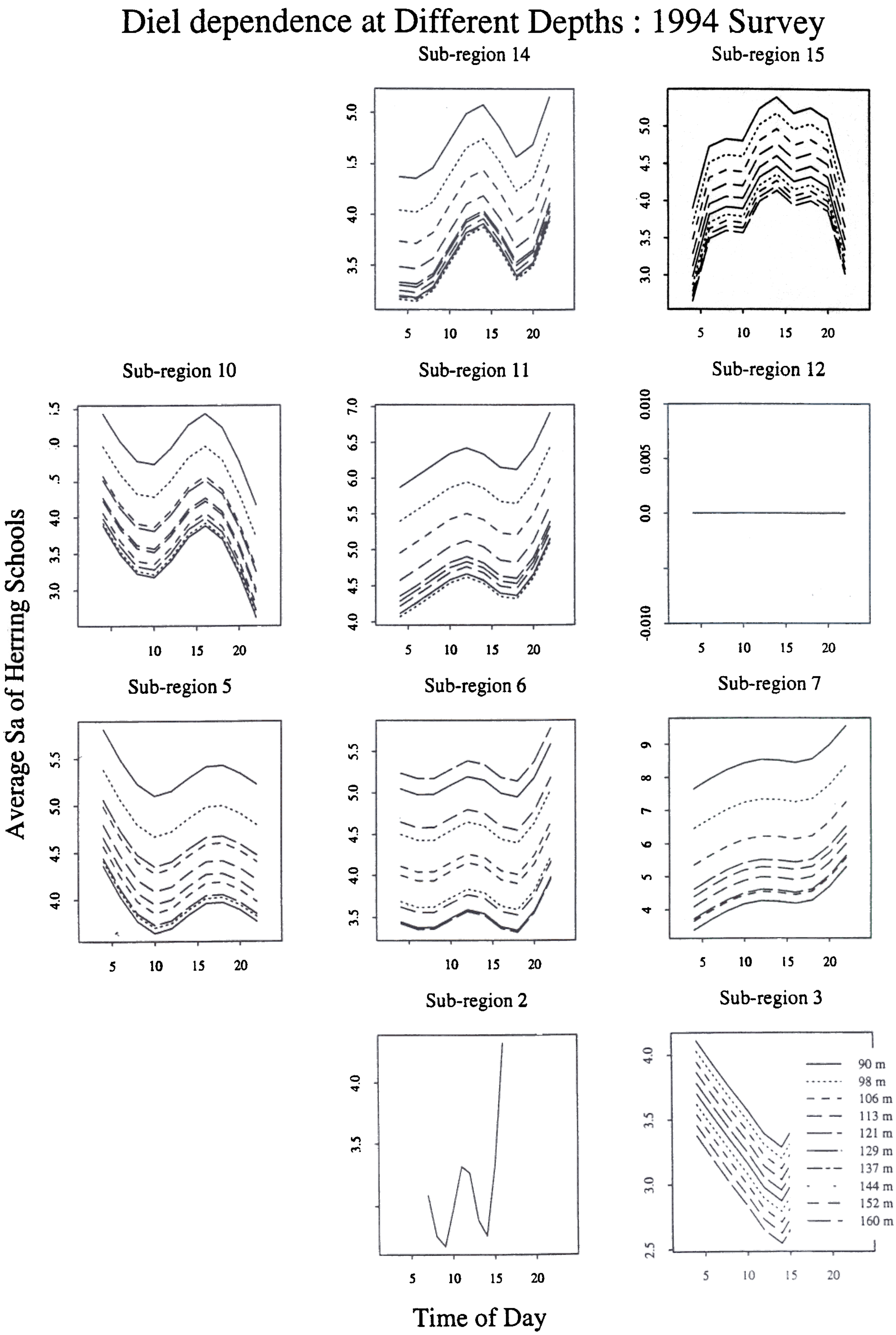

Depth Dependence at Different Times of Day: 1994 Survey
Sub-region 14
Sub-region 15
Sub-region 10
Sub-region 11
Sub-region 12
Sub-region 5
Sub-region 6
Sub-region 7
Sub-region 2
Sub-region 3
Average Number of Herring Schools
Bottom Depth

Figure 8



Diel dependence at Different Depths : 1994 Survey
Sub-region 14
Sub-region 15
Sub-region 10
Sub-region 11
Sub-region 12
Sub-region 5
Sub-region 6
Sub-region 7
Sub-region 2
Sub-region 3
Average Sa of Herring Schools
Time of Day
90 m
98 m
106 m
113 m
121 m
129 m
137 m
144 m
152 m
160 m

D pth d pendenc at D ff rent T m o Day 4 Surv y

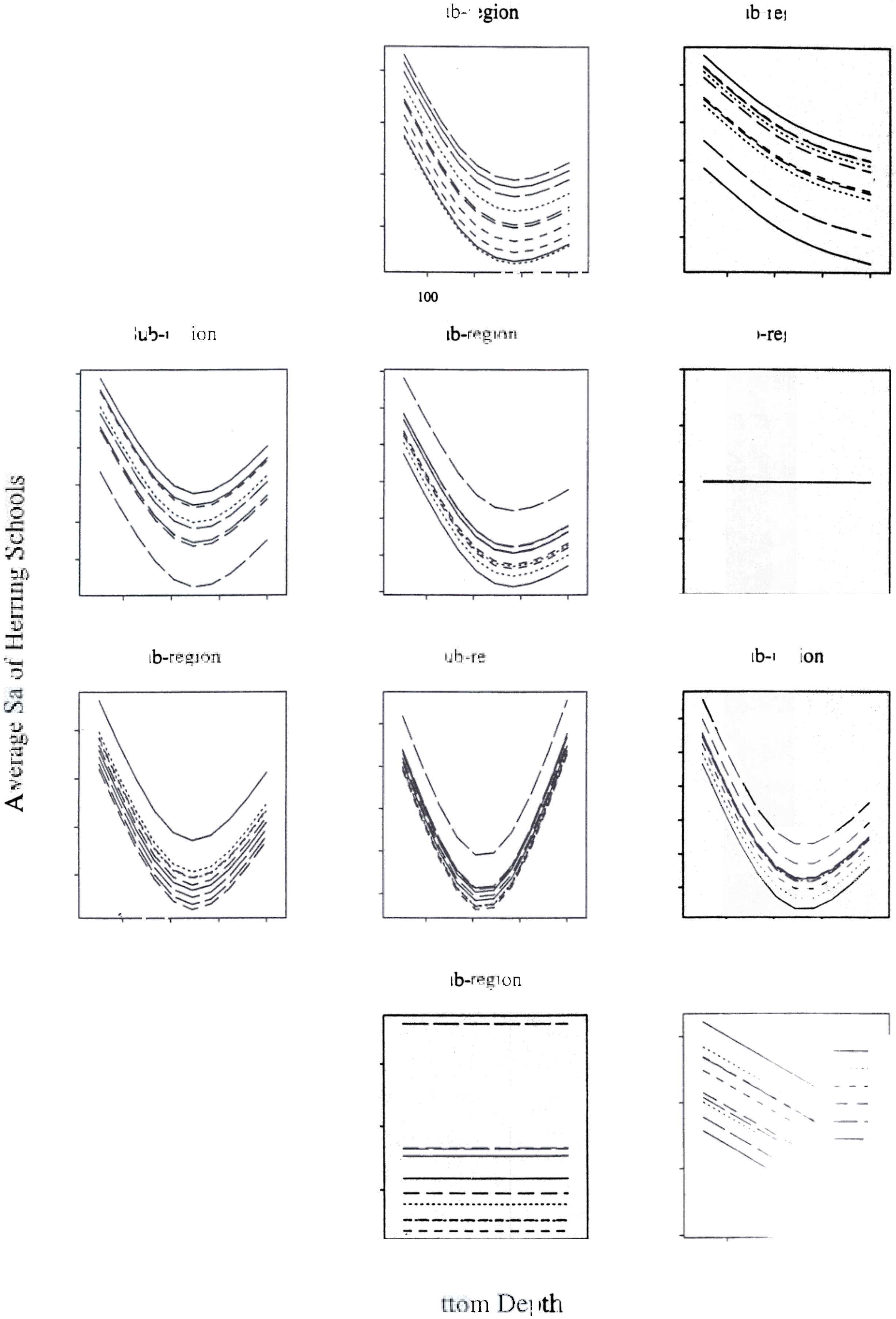
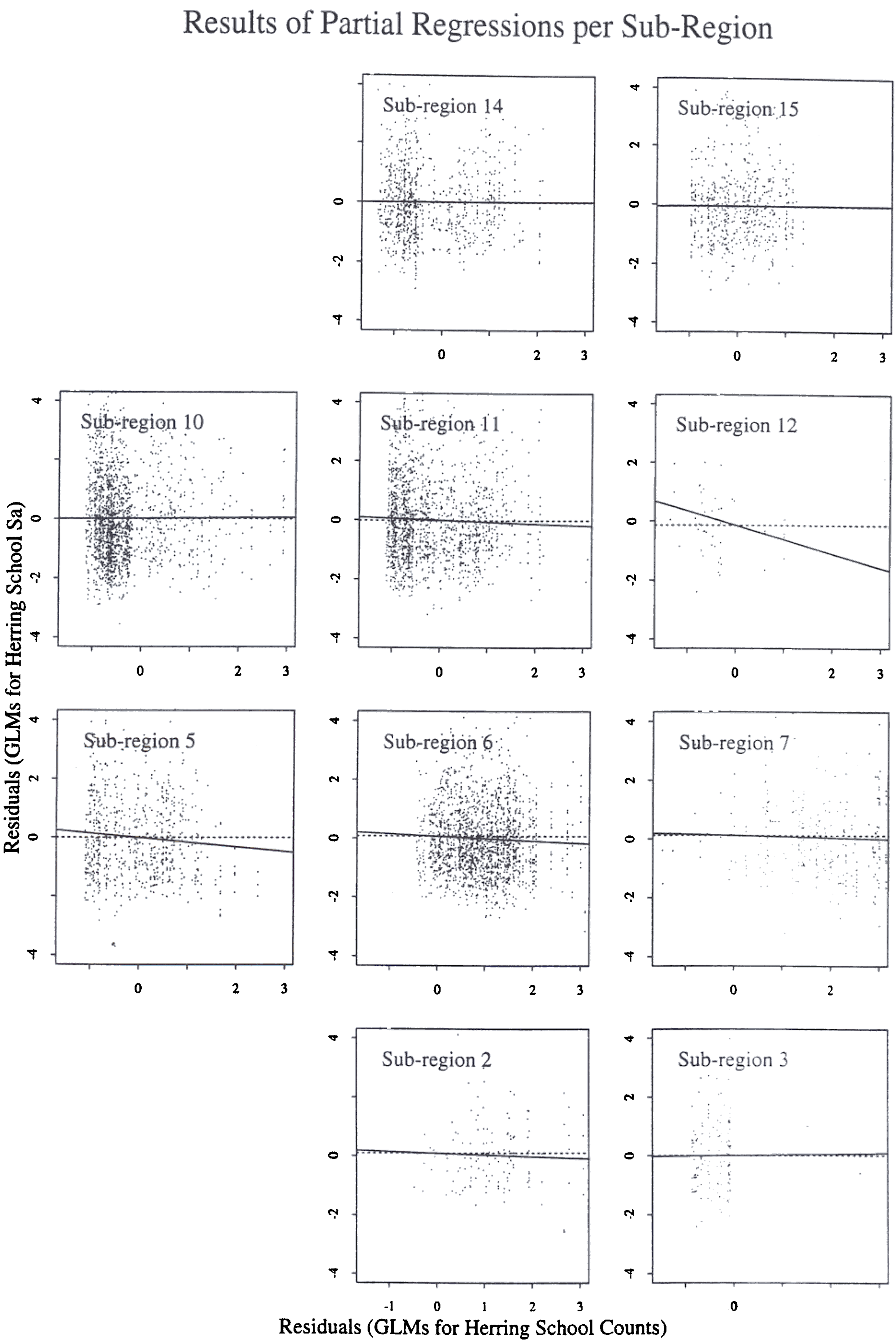


Figure 10


Results of Partial Regressions per Sub-Region
Sub-region 14
Sub-region 15
Sub-region 10
Sub-region 11
Sub-region 12
Sub-region 5
Sub-region 6
Sub-region 7
Sub-region 2
Sub-region 3
Residuals (GLMs for Herring School Sa)
Residuals (GLMs for Herring School Counts)