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Spatio-temporal patterns in herring (*Clupea harengus* L.) school abundance and size in the northwest North Sea: modelling space–time dependencies to allow examination of the impact of local school abundance on school size

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As part of the EU-funded project "CLUSTER" a database was constructed of herring schools identified during a series of acoustic surveys in the northwest North Sea. Among other descriptors, the database included each schools' height, length, and acoustic backscattering energy (S_a). The number of schools per nautical mile. EDSU (Elementary Distance Sampling Unit) was also recorded. The relationships between local school count and school backscattering energy to time-of-day and location were first modelled using multiple regression techniques. The results indicate a considerable degree of non-linear dependency on both time-of-day and location. Herring-school counts per EDSU tended to be high during the middle part of the day and lower at dawn and dusk and were higher along the continental shelf edge about 130 m west of Orkney and Shetland. The regression models, by definition, also allow variability due to each explanatory variable to be assayed and divided. This feature meant that their output could be used to explore further into the relationships among the schools. In this paper the residual variability from the regression models is used to describe density-dependent relationships among herring schools, i.e. we asked "To what extent does local herring school abundance influence the size (backscattering energy) of a given school?" It is concluded that herring school size is regulated mainly by location and time-of-day and that "measured" school size is not influenced by the local "school count per EDSU". The results and their implications are discussed.

Keywords: Generalized Additive Modelling, herring, North Sea, school abundance and size.

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Introduction

The schooling behaviour of pelagic fish has been extensively studied in the laboratory but very little attention has been paid to schooling in the wild (Pitcher, 1993). However, as Pitcher points out, understanding of schooling is fundamental to our assessment and management of commercial fish stocks because the aggregation pattern will impact on catchability and effort measurements. Observations of schooling behaviour in the wild have been mainly dependent on the use of acoustic instrumentation viz. sonars or echosounders (Misund, 1997; Reid, 2000). Extensive studies have been carried out using sonar observations (Hafsteinsson and Misund, 1995; Misund and Jakopsstovu, 1997; Nottestad *et al*., 1996; Misund *et al*., 1995). The main drawback of sonar observations is that they are labour- and vessel-intensive to collect and often difficult to interpret, particularly in terms of school biomass. Their main advantage is that they provide three dimensional (3D) views of each school. Echosounders, by contrast, can provide a great deal more data (see Reid, 2000; Reid *et al*., 2000). The observed schools can be quantified using standard methodologies (MacLennan and Simmonds, 1992). Their main disadvantage is that they provide only 2D information on the structure of observed schools. Use of image-processing technologies (Reid and Simmonds, 1993; Swartzman, 1997; Richards *et al*., 1991; Scalabrin and Masse, 1993; Haralabous and Georgakarakos, 1993) has allowed the collection of extensive databases of pelagic fish school structure from a wide range of acoustic survey situations. These can then be used to answer detailed questions about the schooling behaviour of pelagic fish and its impact on assessment and management.

This concept inspired the EU-funded "CLUSTER" project (1997–1999). The goal of "CLUSTER" was to characterize schooling behaviour among a range of European pelagic fish species using data collected during acoustic surveys (Reid *et al*., 2000). One of the most interesting questions that can be asked of these data is what, if any, factors govern the sizes of fish schools in any particular area. In this paper we have focused on the question of density dependence. This can be expressed as an hypothesis:

> "*In a particular area and at a particular time of day, herring schools tend to be smaller when the number of schools is more numerous.*"

Which is based on the common observation on acoustic surveys that "big" schools tend to be seen in isolation whereas the smaller ones come in groups. One explanation for this phenomenon postulated by Soria *et al.* (1998) is that given fish schools are dynamic and likely to form and break up regularly, the large, isolated schools might represent the aggregated phase and the groups of smaller schools might represent the disaggregated phase.

To examine this hypothesis we used acoustic survey data collected by the Aberdeen Marine Laboratory in the northwest North Sea in July 1991 and 1993–1997 (Figure 1). The surveys covered the waters surrounding Orkney and Shetland. The most abundant pelagic fish are herring, *Clupea harengus*. The analysis initially examined how location and time-of-day influenced the number and size (backscattering energy – S_a) of the herring schools detected. Location is clearly a primary factor, as any fish population will tend to be distributed heterogeneously. Time-of-day is well known to impact on schooling, since schools break up at night and re-form during the day (Freon and Misund, 1999). Given these relationships we have examined how the size of each school was related to the number of schools recorded in an area, the "school count per EDSU". The first part of the analysis allowed us to predict both the size of a school for a particular area and time, in addition to the "school count per EDSU" for a particular time and area. The second step then examines whether any variability from the expected school sizes can be attributed to the number of schools in the EDSU. This can be seen as analogous to the common question in ecology of whether individual animals or plants are larger or smaller at high or low population densities. The first step involved using regression models (Hastie and Tibshirani, 1990; McCullagh and Nelder, 1989) to remove, or at least reduce, the location and time-of-day effects. The relationship of school size to local school count, given a specific location and time-of-day is then examined using the residuals from these models.

Materials and methods

Acoustic surveys and data

The analysis used data from six acoustic surveys carried out in 1991 and 1993–1997. The surveys were all carried out in July and covered substantially the same area (Orkney/Shetland area), and used the same survey dates (Table 1) and the same vessel – FRV "Scotia". The acoustic data were collected using a Simrad EK500 38-kHz echosounder, and 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 echosounder transmission.

Information on each school was then extracted using image-processing software (ImagePro Plus, Media Cybernetics). This procedure combined automated, image-filtering algorithms with interactive decisions made by the user (Reid and Simmonds, 1993). The detection threshold was set at -60 dB, which provided the optimum effective beam angle for the school-volume backscatter (Sv) of the schools retained. The *effective* beam angle 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 ($-25<\Delta Sv>-10$ dB) the beam is relatively large but insensitive to variations in the ΔSv (see chapter 5 in Reid, 2000). Following thresholding, a single morphological filter pass was used to eliminate small objects and smooth the outlines of the larger ones. Previous experience has shown that this combination best preserved school morphology and biomass. The remaining detected objects are identified as schools and labelled by species.

Acoustic data were collected continually during the survey (Figure 1). The data were then divided into one nautical mile EDSUs (Elementary Distance Sampling Unit). One mile EDSUs were used as these satisfied the criteria defined in Simmonds *et al.* (1992) of minimizing the correlation between the fish energies recorded in successive EDSUs. The herring schools in each

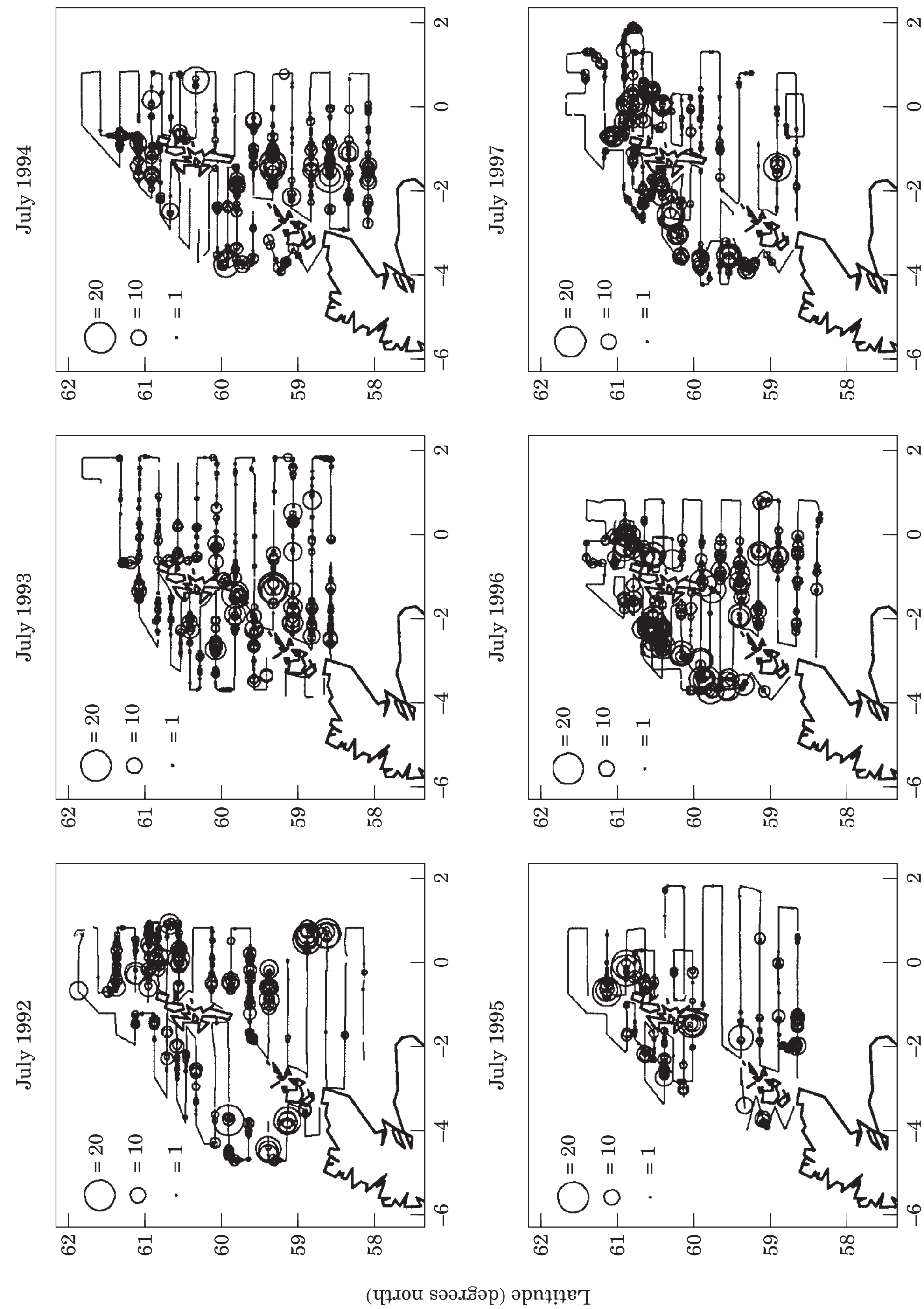

Figure 1. Location of the Marine Laboratory, Aberdeen, acoustic-survey data in July (1991, 1993–1997. Circles represent the number of herring schools recorded.

Table 1. Timing of the July acoustic surveys between 1991 and 1997.

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

EDSU were counted and characterized in terms of their morphology, energy, location etc. The energy from the school was characterized by the S_a value (the area back-scattering coefficient). Physical characteristics of each EDSU were also recorded, e.g. mean depth and sea surface temperature per EDSU (Reid *et al*., 2000).

Throughout this paper we have used the term "school count per EDSU" rather than school *density* per EDSU. While this may appear to be a non-standard terminology, it has been adopted to avoid confusion between the density of fish in the schools and the density of the schools in the EDSU.

Statistical analysis

The analysis is centred on the "school count per ESDU" and the associated backscattering energy (S_a) of each school. The "school count per EDSU" (1 nmi) was used as an expression of the local school density; in this case the number of schools per nautical mile. An alternative would be to use the distance to the nearest neighbouring school (NN). NN, however, is an expression of extremely local school abundance, whereas the "school count per EDSU" represents the school density over a wider scale and was chosen as representing the *general* situation of each school rather than simply its proximity to its nearest neighbour. It is known that fish abundance parameters are dependent on many different factors such as depth, longitude, and time-of-day and that these factors can interact with each other. Regression models are a useful choice for quantifying such variability and were used here (McCullagh and Nelder, 1989; Bailey *et al*., 1998; Beare *et al*., 1998; Daskalov, 1999; Venables and Ripley, 1994; Lindsey, 1995). After experimentation, the count data ("school count per ESDU") and the continuous data for the school backscattering energy (S_a) were modelled using Generalized Additive Models (GAMs) which are now widely used in fisheries science (Hastie and Tibshirani, 1990; Augustin *et al*., 1998). In additive modelling, the dependent variable (e.g. "school count per EDSU") is interpreted as a random function Y(y1, . . ., yn, . . .) where each observation is a random variable and all observations are assumed to arise from the same probability distribution. GAMs account for the dependence of the mean on various covariates. The effect of the covariates on the mean is estimated using non-parametric smoothing functions: locally-weighted regressions were used in this case because they can be fitted successfully in multiple dimensions. In effect, the data themselves dictate how the shape of the dependent variable is affected by each covariate. Clearly the resolution and distribution of the original data themselves in time and space is crucially important.

The models had the following general structure:

Count per EDSU = smooth(Longitude, Latitude, Time of Day) + Error . . . (a)

Backscattering energy (S_a) = smooth(Longitude, Latitude, Time of Day) + Error . . . (b)

The Poisson distribution is often considered to be appropriate for describing the error structure in count data (Lindsey, 1995). However, preliminary application of GAMs from the Poisson family to the count data tended to produce over dispersed models with unacceptably high residual variation (Lindsey, 1995). The Poisson distribution assumes that the mean is equal to the variance [$\mu = \mathrm{Var}$]. When the variance exceeds the mean (i.e. very high residual deviances) then the data are not Poisson distributed. The excessive residual variability, caused by aggregation of the data in space and time makes discrimination between models using conventional chi-square or Akaike Information Criterion (AIC) tests unreliable. Methods for correcting over-dispersion in Poisson models are available (see McCullagh and Nelder, 1989; 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 GAMs with a negative binomial error structure (Venables and Ripley, 1994; Lindsey, 1995) which assumes that $\mu = \mathrm{Var}^2/\theta$. The parameter θ, which is a measure of aggregation too, can be estimated from the data using maximum likelihood techniques. Data for school acoustic backscattering energy (S_a) were also modelled with GAMs, but Gamma error was considered more appropriate as school S_a data are highly skewed and always positive. Nonlinear dependence was described in all models using locally weighted regression smoothers. The data from each of the six surveys were modelled separately, allowing the spatio-temporal patterns used in each case to be different.

Assessing model adequacy in GAMs is difficult, and cannot be entirely objective but it essentially follows an analogous procedure to ordinary linear regressions except that a generalization of the variance, known as "deviance" is used instead (Venables and Ripley, 1994). In statistical modelling the typical aim is to obtain a balance between explaining all or none of the variance

Table 2a. The numbers of observations made during each acoustic survey.

Survey	1991	1993	1994	1995	1996	1997
n	2221	2234	2364	2052	2140	2239

Table 2b. The numbers of herring schools observed during each acoustic survey.

Survey	1991	1993	1994	1995	1996	1997
Schools	1672	1423	1388	816	1792	1863
Schools/n	0.75	0.64	0.59	0.40	0.84	0.83

(deviance). A model with a residual deviance of 0, for example, has an R^2 of 100% but is identical to the original data and not a summary. As a general rule we searched for models in which the residual deviance was similar in magnitude to the residual degrees of freedom. The GAM for counts of herring per EDSU in the 1991 data, for example, has a "Null" deviance of 6074 and a residual deviance of 2611 (see also Table 3a). To calculate the Null deviance the counts are fitted to their average (the intercept). In other words the Null deviance describes the total amount of variability in the data when no explanatory covariates are used at all. This demonstrates that the combined effect of location [smooth(long,lat)] and time-of-day [smooth(time)] on average herring-school count, reduced the deviance by 3463 ($6074 - 2611$) in this example. The total degrees of freedom are 2221 ($n - 1$), while the residual degrees of freedom are 2130 which means that 38 [3463/($2221 - 2130$)] units of deviance are explained by the model for each degree of freedom used which is highly significant. The model has an R^2 of 41% which means that most (59%) of the variation in the average count per EDSU remains unexplained. Nevertheless, inspection of the residuals suggests that the model is "adequate" and useful for our current purposes.

Results

Statistical analysis

Sampling intensity was similar during each of the six surveys (Table 2a), although the numbers of herring schools recorded varied substantially (Table 2b). In 1997, for example, 1863 herring schools were seen in 2239 EDSUs, while in 1995 only 816 schools were seen in 2052 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).

The locations of the data from the six surveys are illustrated in Figure 1 and clearly the spatial coverage was slightly different from year to year. The survey track extended further south in 1991 and 1994 (Figure 1) and further west in 1993, 1995 and 1997 (Figure 1). Spatial distributions of school abundance also varied between surveys. In July 1991 most schools were seen northwest of Shetland. In 1993 and 1994 the highest school counts were noted in the Fair Isle channel while more recently (1995, 1996, and 1997) schools were most prevalent to the west of Orkney and Shetland between the 100 m and 200 m depth contours.

The GAM fits to the school count data for 1991 and 1993 July surveys are summarized as examples in the analysis of deviance tables (Table 3a,b) below. Terms fitted are described using S-plus notation. "Lo" refers to locally weighted regression smoothers (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 tested whether that reduction in deviance was statistically significant given the concomitant increase in model complexity (degrees of freedom). In the case of the 1991 survey data, the third model was chosen. Residual deviance was reduced by 490 from 3102 to 2611, using 11 less degrees of freedom (see Table 3a).

The analysis of deviance tests between models 1 and 2 gauged whether time-of-day explained significant quantities of deviance (variance) when covariables of location were also included. The test between models 2 and 3 ascertained whether the effect of longitude depended on latitude when time-of-day was included. The last test, between models 3 and 4, tested whether the effect of time-of-day depended simultaneously on longitude and latitude. In other words the last model allowed the spatial pattern of school occurrence to vary with

Table 3a. The results of Generalized-Additive-Model fits to herring-count data for 1991. (NB, smoothing span=0.06).

Terms	Resid d.f.	Resid dev	Test	d.f.	Dev	Pr(F)
1. Lo(Lon)+lo(Lat)	2149	3940				
2. Lo(Lon)+lo(Lat)+lo(Time)	2119	3102	+lo(Time)	30.7	838	<0.01
3. Lo(Lon,Lat,)+lo(Time)	2130	2611	2 vs. 3	− 11	490	<0.01
4. Lo(Lon,Lat,Time)	2147	3276	3 vs. 4	− 17	− 664	<0.01

Table 3b. The results of Generalized-Additive-Model fits to herring-count data for 1993. (NB, smoothing span=0.06).

Terms	Resid d.f.	Resid dev	Test	d.f.	Dev	Pr(Chi)
1. Lo(Lon)+lo(Lat)	2159	3584				
2. Lo(Lon)+lo(Lat)+lo(Time)	2128	3164	+lo(Time)	31	420	<0.01
3. Lo(Lon,Lat,)+lo(Time)	2147	2874	2 vs. 3	− 19	290	<0.01
4. Lo(Lon,Lat,Time)	2163	3389	3 vs. 4	− 16	− 515	<0.15

time-of-day, and then tested whether this model was an improvement (statistically) over the one where the spatial pattern was the same at each time-of-day. For all six surveys (1991, 1993–1997) 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 "school count per EDSU" did not vary with time-of-day, only the average level changed. Put another way, the relative numbers of schools was consistent between areas irrespective of time-of-day.

In Figure 2 the model output at 1000 Greenwich Mean Time (GMT) is plotted for each survey in the left-hand panel. In the right-hand panel, mean "school count per EDSU" is plotted calculated over nine surfaces predicted from the model at 400, 600, 800, 1000, 1200, 1400, 1600, 1800, and 2000 GMT. "School count per EDSU" tended to be highest in the late morning. The equivalent of model 3 (Table 3a), but with Gamma error, was chosen to summarize the herring-school acoustic backscattering energy (S_a) data. The spatial pattern (Figure 3) was inconsistent between surveys, although schools did tend to be larger around Shetland and in the southern part of the study area in most years. Herring schools were also larger in the evening and smallest in the early morning. It should be noted here that the average school energy is not necessarily related to the total herring biomass. Figure 3 provides a summary of where the largest herring schools are located and at what time of day, but not necessarily where there is high herring biomass.

Partial regressions

The aim of the modelling described above was to account for the variability in school-count per EDSU and school S_a in relation to location and time-of-day. The residuals from these models represent remaining unexplained variance. They were plotted against each other and the results are presented in Figure 4. A linear model was fitted through these data by least squares. A negative slope would suggest negative density dependence and *vice versa*. The plots in Figure 4 show that herring school backscattering energy (S_a) recorded during all six surveys was completely independent of local school count. In other words, the size or backscattering energy of a herring school at a known point in space and time within the survey region does not depend on local school count.

Discussion

The partial regression approach described here may seem unnecessarily laborious. It must be remembered, however, that our aim was to extract a signal from data that exhibited complex non-linear and multivariate dependencies. Only by first accounting for variability due to time and space could we be reasonably confident that any residual variability might be due to another specific factor, e.g. the "school count per EDSU". Additionally, the first stage of the analysis allowed a detailed quantification of the space – time dependencies in the data, which can be regarded as useful in itself.

The initial hypothesis we proposed was that, "In a particular area and at a particular time, herring schools tend to be smaller when they are more numerous". The hypothesis is based on frequent observations on acoustic surveys but cannot be confirmed by the current study. A cursory examination of the data does, however, appear to support the idea. When "school count per EDSU" (or school-nearest-neighbour distance), for example, is plotted directly against school backscattering energy, it

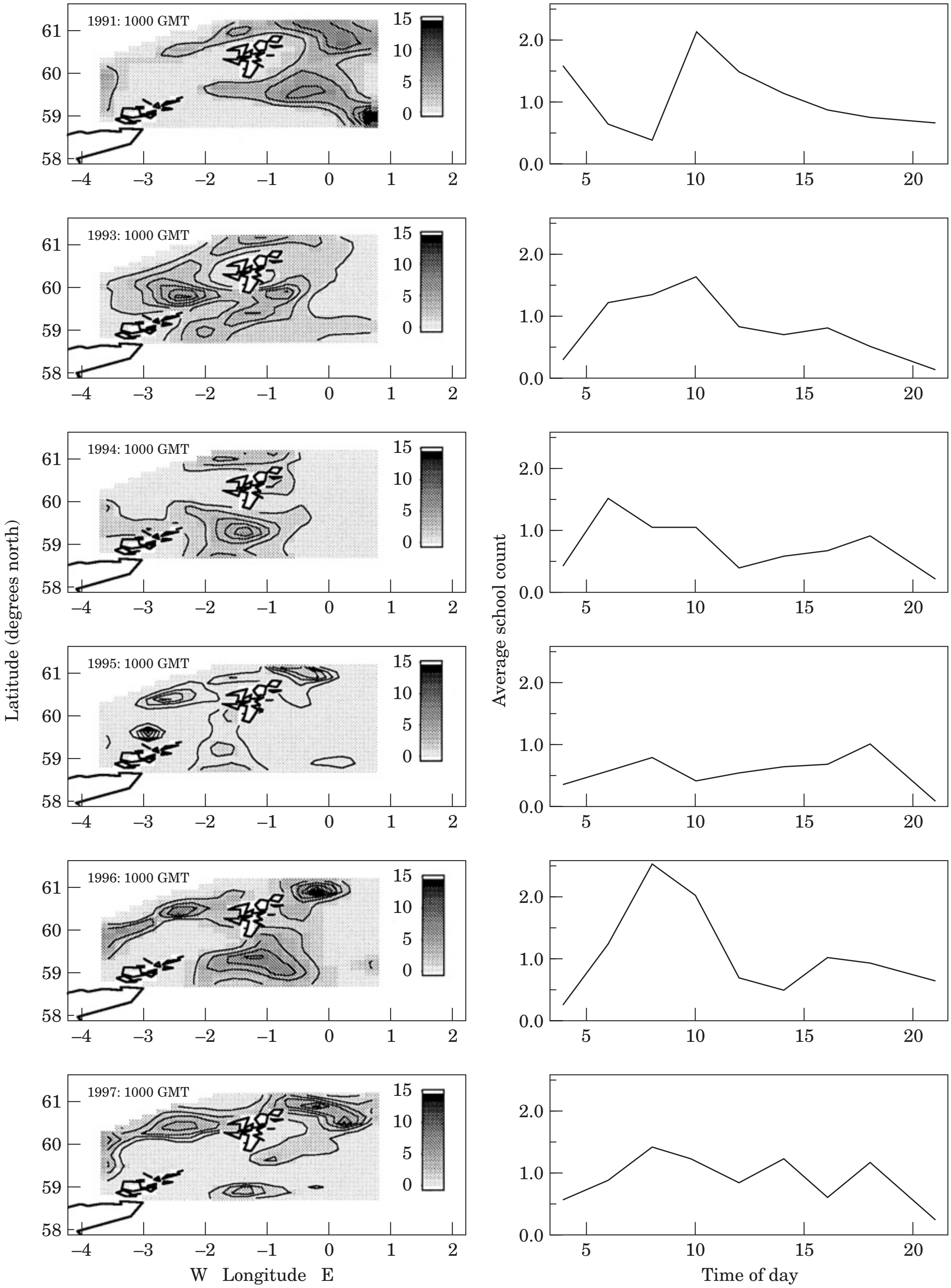

Figure 2. Left panel: spatial pattern in herring – "school count per EDSU" at 1000 GMT recorded in the survey area in July 1991, 1993–1997. Right panel: diel dependency of average "school count per EDSU".

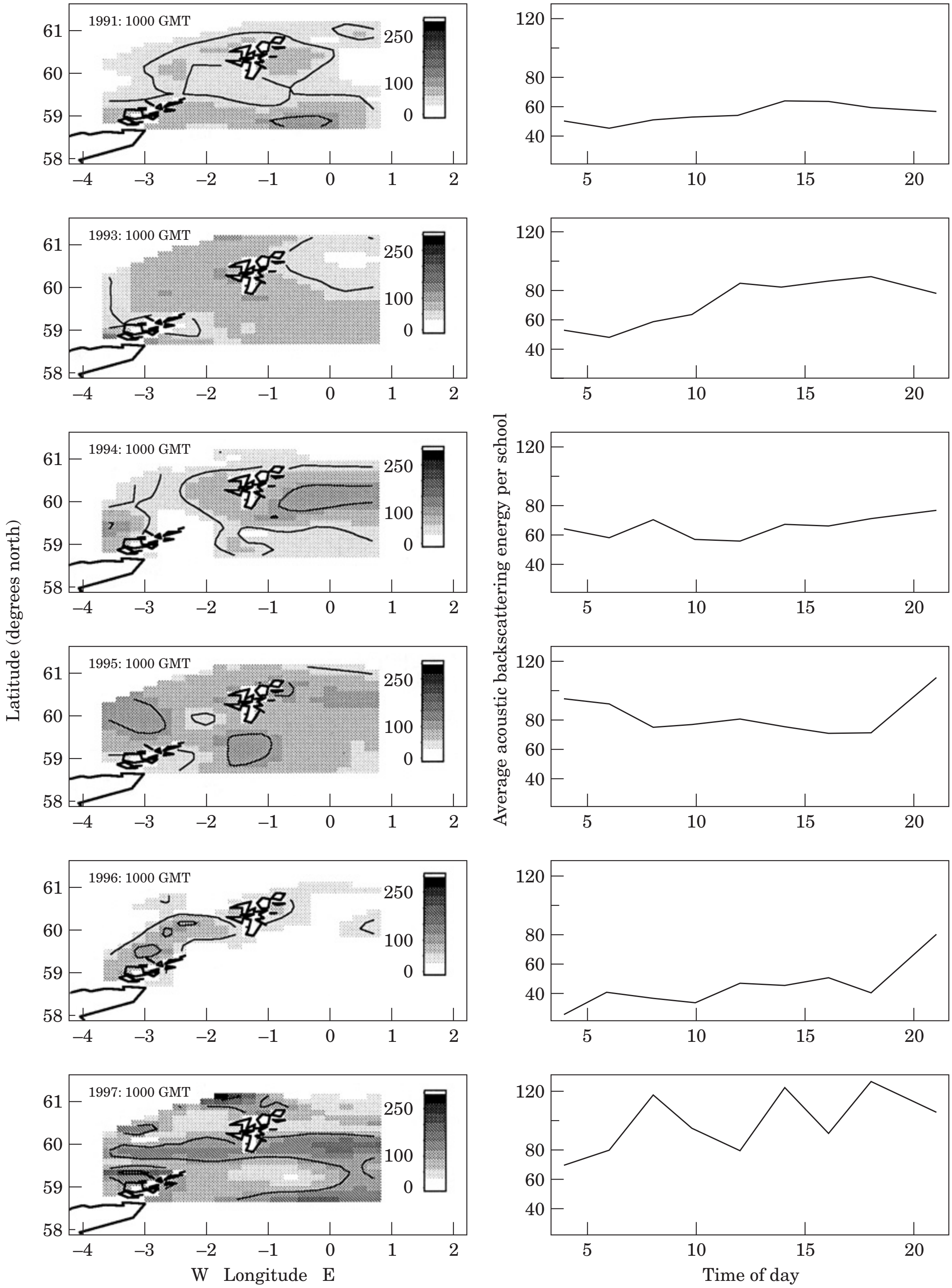

Figure 3. Left panel: spatial pattern in herring-school backscattering energy per EDSU at 1000 GMT recorded in the survey area in July 1991, 1993–1997. Right panel: diel dependency of average school backscattering energy per EDSU.

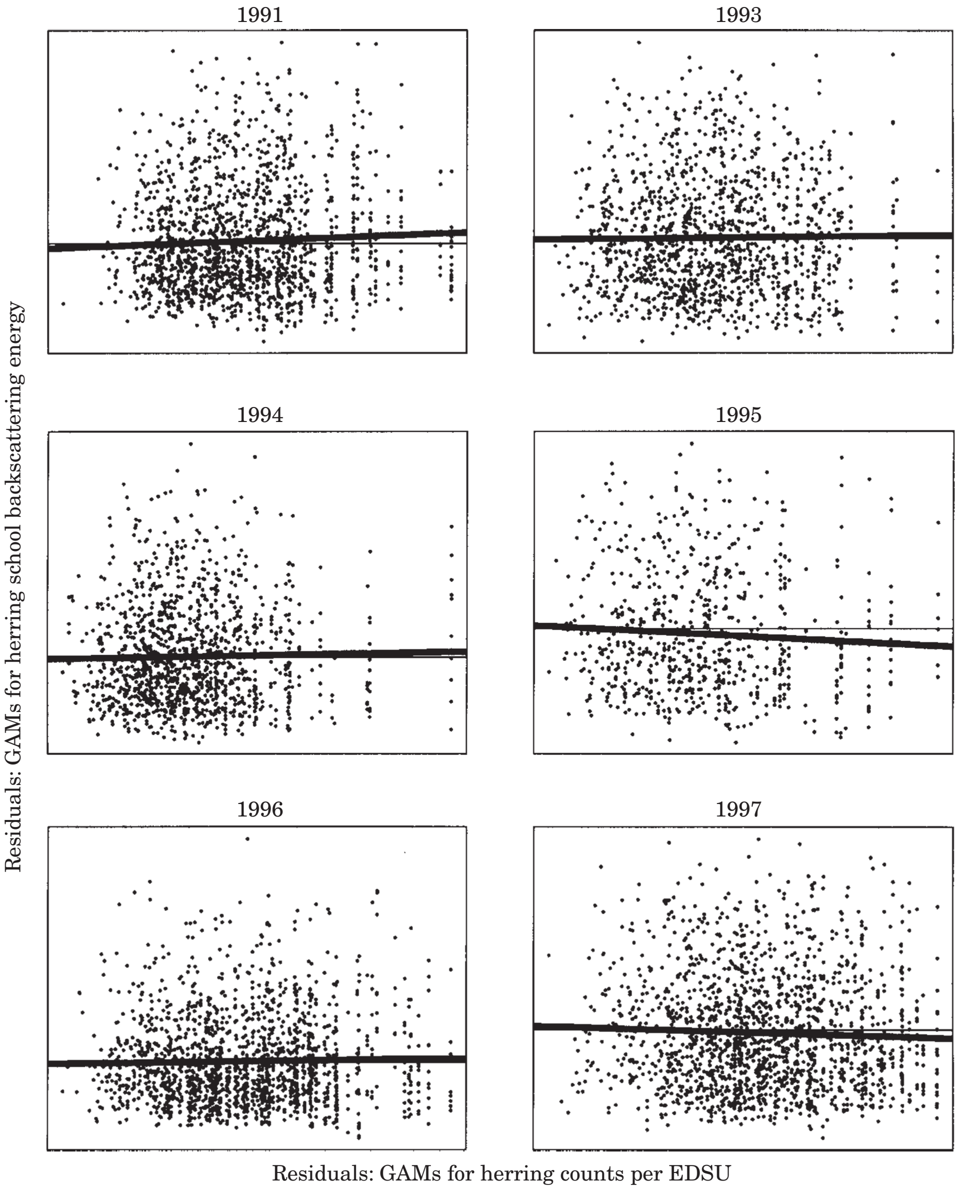

Figure 4. Density dependence in the herring schools. Note: none of the linear regression models have statistically significant gradients of either sign.

appears that the EDSUs with high school counts tend to be associated with smaller schools and *vice versa*. This negative relationship between the two parameters is, however, the result of time-of-day and location effects rather than any putative "density dependence". A bivariate plot between the two quantities, therefore, is a potentially serious oversimplification and needs to be interpreted carefully.

In the early part of the day, for a location with reasonable amounts of herring, there is a tendency to see more and smaller schools. Later in the day there are, typically, fewer, larger schools. When multivariate models are used to reduce effects due to time-of-day and location, the residual variability shows no relationship to "school count per EDSU". So while there might appear to be evidence in these data that more schools suggest smaller schools, we believe that this is due to location and time-of-day effects rather than any direct biotic effect of the school abundance itself.

The important factor appears to be the variation in the number of schools per EDSU over the course of the day. In most years this starts low, reaches a maximum prior to 1200 h, and then declines thereafter. Why should this be so? Herring schools are believed to break up with the onset of darkness (Freon and Misund, 1999) and then start to re-form after dawn. It can probably be assumed that the first schools to form will be small. Therefore, initially, the fish will tend to coalesce into an increasingly large number of small schools. As the day progresses these schools themselves will tend to merge into larger and hence fewer schools. In the first part of the day both these processes can be assumed to be going on at the same time. The first small schools to form are then likely to merge into larger schools earlier than those that coalesce later. This interpretation may be confirmed by the changes in school S_a during the day. In the early morning in most years, the schools were initially small and then tended to increase in size throughout the day. In most years the number of schools then tends to decrease over the remainder of the day. Correspondingly the size of those schools tends to show a slight increase. The most likely explanation for this is that at some point in the first part of the day most of the fish have aggregated into schools. For the rest of the day those schools will continue to coalesce into larger schools. As suggested by Soria *et al.* (1998) these schools will probably merge and break up in a dynamic fashion throughout the day (see also Pitcher *et al.*, 1995). There was a clear tendency, however, for fewer and larger schools later in the day, suggesting that this process was tilted towards aggregation rather the break up of schools. It is also interesting to note that while the number of schools per EDSU and their S_a values changed throughout the day they did so in a consistent fashion across the whole area in any given year. This was illustrated by the analysis of the relative improvements between models 3 and 4 using position and time either as additive or as interactive factors. This suggests that the process of school formation and the subsequent merging of schools was generally quite robust and not subject to local variation in other conditions.

There has been some previous work on density dependence in schooling pelagic fish, although usually at a population scale. Paloheimo and Dickie (1964) first raised the issue of density-dependent catchability in pelagic fish. They suggested that pelagic fish may reduce their spatial extension to maintain constant density within schools. The present analysis has examined a similar question at a more localized level. Petitgas and Lévénez (1996) found that the biggest schools were randomly positioned relative to other schools and that their proportion varied with the survey abundance. Marchal and Petitgas (1993) found that there was no evidence for a relation between the number of schools and the biomass in the EDSU. They also found, however, that the probability of encountering a large school was slightly increased with a high "school count per EDSU". Based on the current work the most likely scenario is that any observed density dependence is most likely the result of time-of-day and location effects.

The conclusion must be that there was no evidence for any density-dependent effect in herring school S_a. Nevertheless there is strong evidence that both "school count per EDSU" and the S_a values of those schools does change during the course of the day. The process of school formation from the night-time situation of scattered fish continues throughout the early part of the day. The number of schools per EDSU rises throughout this period. One inescapable conclusion from this is that school-based echointegration may tend to underestimate herring abundance during this period. Acoustic surveys for herring in the North Sea are deliberately discontinued during the hours of darkness recognizing that schools break up in darkness. However, a possible implication of this study is that the surveys should not be started until the process of school formation is substantially complete.

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