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SPATIO-TEMPORAL PATTERNS IN PELAGIC FISH SCHOOL ABUNDANCE AND SIZE: A STUDY OF PELAGIC FISH AGGREGATION USING ACOUSTIC SURVEYS FROM SENEGAL TO SHETLAND

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ABSTRACT

As part of the EU funded project CLUSTER, databases were constructed of pelagic fish schools identified during a series of acoustic surveys in the NW North Sea, Bay of Biscay, western Mediterranean and Agean Seas and off Senegal. Among other descriptors, the databases usually included the height, length and energy (S,,) of each school. The number of schools per 1 nmi EDSU 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 in some of the surveys on time of day and water depth. School count per EDSU tended 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 and year. Possible explanations for such patterns and the differences and similarities between the survey areas will be discussed, as well as the impact of these findings on the conduct and analysis of acoustic surveys. In addition, we have examined the spatio-temporal pattern of sampling in each of the survey series and we will present an analysis of the impact of survey design on the potential for such spatio-temporal modelling studies.

INTRODUCTION

During the European Union funded project CLUSTER (FAIR CT 96.1799) information on pelagic fish schools was collected together into a single database for use by all partners in the project (Reid et *al.,* 2000). The geographic range of these data, in particular, make them an extremely important and useful scientific resource. Altogether there are data available for 39 separate acoustic surveys in the NW North Sea, Bay of Biscay, western Mediterranean and Aegean Seas and off Senegal, West Africa. Among other descriptors, the data-set for each survey usually includes the height, the length and the acoustic backscattering energy (S_a) of each school encountered. Numbers of schools per 1 nmi (EDSU; Elementary Distance Sampling Unit) are also recorded. The objective of this particular study was to build a simple framework based on stochastic models which would allow us to compare and contrast some of the most important measurements made on pelagic fish schools ranging from Senegal to Shetland.

The following two response/dependent variables are considered:

1. Counts of fish schools per 1 nm sampling unit (Elementary Distance Sampling Unit, EDSU);

2. Acoustic back-scattering energy (S,) of each school encountered.

The paper is divided into two sections and each summarises the same information using a different data-analytical protocol. In Section I, the 'raw' dependent variables are assessed as functions of time of day and bottom depth, using a separate model for all 39 different surveys. In Section II the data are first simplified into a single matrix by aggregating the data into averages which is then summarised using a single multiple regression model.

METHODS

All of the following analyses were done using programs supplied as standard in S-plus, Version 5.1.

Section I: Modelling Dependency on Time of Day and Bottom Depth

Counts per EDSU

Data from the track of an acoustic survey are typically divided into 15 minute time-intervals (EDSUs) and the number of fish schools detected by echo-sounder within each can be counted., The dependence of such counts on external variables (predictor variables or covariates) was then summarised using regression techniques. Since fish schools are distributed thinly, the majority of EDSUs sampled return zero counts and such data are clearly unsuitable for standard linear regression models which assume symmetry in the dependent variable. Our solution was to use Generalised Additive Models (GAMs) which are applicable to count data with zeros (Venables and Ripley, 1994).

After experimentation, GAMs with error distributions from the Quasi family were fitted via locally-weighted regression smoothers to the school count data from each of the 39 surveys (McCullagh and Nelder, 1989). In all models (Quasi) the mean school count was set to be equal to the variance which is analogous to a model from the Poisson family. The Quasi distribution was preferred over the Poisson, however, since the 'over-dispersion', caused by clumping (non-independence) of the data in space and time is accommodated in the subsequent F-tests between nested models that are used during model-selection (McCullagh and Nelder, 1989). Further tests of adequacy were done by examination of the residuals and by plotting the output of the models against the raw data. The latter procedure is useful where sampling inconsistencies indicate that modelled values are unsupported by any actual observation.

School acoustic back-scattering energy (S,)

Using software developed during CLUSTER (Reid et *a/*,, 2000) an estimate of the acoustic back-scattering energy of each individual fish school was made. Every time a school was detected, its S_a was measured. The S_a quantity reflects both the physical size of a school and the number of fish it contains. Histograms showed that the S_a data had skew frequency distributions and were similarly (viz count data) unsuitable for modeiling using standard linear regressions. After experimentation, acceptable models were found in the form of GAMs incorporating the Gamma error distribution.

Model-selection

Biases that might arise from non-random sampling (confounding) were assessed for each survey,, prior to formal modelling by plotting the time of day against bottom depth. Data-voids and sampling inconsistencies emerge from such procedures and the credibility of the relevant model outputs can be assessed (Beare and McKenzie, 1999a, b). It should be noted that for some of the surveys, even this simple information (viz dependence of school count and/or S_a on time of day and/or bottom depth) is unavailable because of non-random sampling. In one data-set, for example, sampling at less the 40 m bottom depth was done in the evening. This type of sampling renders the effect of time of day and bottom depth on the dependent variables (school count and/or S,) inseparable from each other.

After assessing the degree of confounding by visual examination of the data, time of day and bottom depth were fitted to each response variable separately (school counts and S,) using GAMs. A series of nested models then allow us to assess the following:

whether time of day and bottom depth explained significant quantities of variability

2 whether the shape of that dependence was non-linear; and finally

3 whether there was any interaction between the covariates

Significant interactions, selected for the majority of surveys, imply that the shape of the time of day dependence pattern varies with bottom depth and vice **versa.**

The objective of the data-analytic procedure in Section I was to identify how school count per **EDSU** and the respective acoustic back-scattering energy of each school depended both on the time of day they were recorded and the bottom depth in 39 different surveys, covering an extensive geographic area. [Note: each EDSU is a 15 min aggregation, but acoustic data are actually collected almost continuously. ‘Time of day’ then refers to the mid time point recorded per EDSU and the bottom depth is also averaged per EDSU].

In Section I, procurement of well-fitting models, in terms of propinquity of modelled values to raw data values, assumed a secondary importance. The CLUSTER data are observational, not generated as part of a designed experiment, and well-fitting models are not necessarily the most desirable summaries. R^2 values of 100% could easily be obtained for these datasets by fitting n-l polynomials, and model values would then pass exactly through each raw data point. Such models, however, would in this case provide poor summaries, poor forecasts and ultimately fail to fulfil our current objectives.

Section II: Attempting a Global Summary of Fish School Abundance Data From Senegal to Shetland

In a second, complimentary approach, we attempted to obtain a further, simpler global summary of both the school count and S_a data. It was done by calculating average school counts and school S_a for each survey (Tables 1 and 2) together with the relevant variance, average depth, latitude and longitude (Tables 1 and 2). For count data the mean/variance ratio is meaningful and was included to be used as an independent (from the total density or count of schools) measure of the aggregation of schools in space and time. Average school counts and school S_a (see Tables 1 and 2) were then modelled with ordinary multiple regression models as functions of average location, depth and degree of aggregation in space. This is a crude approach, but there are many data and our goal is to characterise the most important factors affecting fish school abundance and school size among 39 disparate datasets. The procedure undoubtedly obscures potentially useful detail, but as a global summary it worked well (Results; Tables 1 and 2).

RESULTS

Section I: Modelling Dependency on Time of Day and Bottom Depth

Aberdeen 1991,1993-l 997

The CLUSTER project database included six surveys done during July 1991, 1993-97 by the Marine Laboratory, Aberdeen. The locations of these data to the north of Scotland around Orkney and Shetland are displayed in Figure 1, while the cruise track itself, together with circles scaled to fish school count, is in Figure 2. Selected results from the models are displayed for each of the six surveys in Figure 3. Overall, the relationship between numbers of herring schools and their acoustic back-scattering energies was rather erratic. Generally, mean school counts were higher during the middle of the **day** and were greater in deeper water. No clear pattern emerges from the data for school S,.

The failure to arrive at a clear consensus for the Aberdeen data is, we believe, a result of poorly handled spatial effects in our data-analytic protocol and the especially heterogeneous nature of the bathymetry and hydrography of this particular study area. Subsequent, more detailed analyses of the Aberdeen data-set demonstrate that more reliable information can be obtained, either by dividing the data into smaller spatial compartments, or by modelling the spatial dependencies directly (see Beare et *al.*, This Issue).

Coruna 1991, 1993, 1995-1996

The lnstituto Español de Oceanografia (IEO), Centro Oceanografico de A Corutia supplied data from five acoustic surveys around the lberian peninsular (Figs 1 and 4). The signals from these data were particularly strong and are summarised in Figure 5. Average fish school count per EDSU was highest just before noon and there was some indication from the data that this peak occurred later in the day at greater bottom depths (see Coruna 91 and 93). School S_a tended to be highest at either dawn or dusk and was broadly negatively correlated with average counts.

Dakar 1984, 1985, 1987, 1989, 1992 and 1994

The CLUSTER database also includes a tropical data-set from the west coast of Africa made available via IFREMER, Nantes. Altogether there were data from eight surveys done off Senegal (Fig. 6) between 1984 and 1994. The average number of school counts was comparatively low (Fig. 7) compared with the European data, and the overall pattern of diel activity varied between surveys. In two out of the eight surveys available (March 1984 and April 1985) mean school count peaked in the morning, while in four (November 1984, October 1985, February 1987 and March 1989) the peak occurred in the afternoon. In the last two surveys (February 1992 and April 1994) school count was highest at noon (Fig. 7). Average school S_a in the Dakar data tended to be positively correlated with the school count.

Heraklion 1996 and 1997

Data from two surveys (October 1996 and May 1997) were supplied by the Institute of Marine Biology of Crete (Fig. 8). In 1996, most fish schools were seen in the northern part of the bay in relatively shallow water along the coast, whereas in 1997 EDSUs with high school counts were recorded in the mouth of the bay in much deeper water. In 1996 more schools were seen in the evening and their mean S_a was higher in early afternoon after when it fell sharply (Fig. 9). Conversely, in the October of the following year (1997) more schools were seen in the morning (Fig. 9). The average S_a values were higher in the morning in shallow water (25 m) but higher in the evening in deeper water (55 m; Fig. 9). This is an example of 'interaction', where the shape of day/night dependence changes with depth. The authors believe, however, that in this case the observation is an artefact, probably caused by the non-random sampling revealed in Fig. 16 where time of day is plotted against bottom depth (see Discussion).

It must be accepted that the Heraklion October 1997 dataset inadequate for separating effects of time of day and bottom depth on fish school parameters.

Bay of Biscay 1991, 1992, 1994 and 1997

Acoustic survey data for a large area of the Bay of Biscay was covered during four surveys done by IFREMER and their locations are plotted in Fig. 10. There are two clear aggregations of fish abundance: one between 45-46'N and 1.4-2'W; and the other further south between 44-45'N and 1.5-2'W. Patterns of school count and school S_a as functions of time of day and bottom depth were inconsistent. Where a negative correlation between the two parameters was seen, its sign was opposite to the pattern that might be anticipated. High S_a schools were surprisingly noted in the middle of the day when average school counts per EDSU were at minima (Fig. 9).

North-west Mediterranean Sea (Part I) 1992, 1993, 1995 and 1996

These surveys (Fig. 11) were all done in the late autumn fairly close to the coast, in water ranging from 20-140 m. There was a consistent spatial pattern of fish school occurrence, with two main groupings in the far south-west and north-east of the study-region (Fig. 11). Summaries from the models (GAMs) are supplied in the first four rows of Figure 12. Maximum school counts were recorded in daylight. In 1993, 1995 and 1996 numbers peaked at mid-day while a bimodal pattern was seen in the autumn of 1997. Overall school S_a was not clearly negatively correlated with the school counts and were larger at dusk than at dawn for all surveys (Fig. 12). School S_a also tended to be higher in deeper water (90 m).

North-west Mediterranean Sea (Part II)

Four further surveys from the Mediterranean **Sea** collected in July 1993, 19951997 were analysed (Fig. 13). Average school counts in the area increased with bottom depth while their S_a fell (Fig. 12). Dependence on time of day was erratic. In 1993, 1995 and 1997 minimum school counts were made at noon, whereas in 1996 school count per EDSU peaked at noon. In a pattern entirely opposite to that of the north-west Mediterranean Sea (Part 1) average school S_a was greater at dawn (Fig. 12).

Section II: Attempting a Global Summary of Fish School Abundance Data From Senegal-Shetland

Average school count per survey

The average school counts (Table 1) were log-transformed and then modelled (with a standard linear multiple regression model) as various functions of mean/variance ratio, mean Bottom depth, Distance North (Latitude) and Distance West (Longitude). After considerable experimentation and a 'stepwise' model-selection procedure based on minimising the Akaike Information Criteria (AIC), the following model was chosen using the data in Table 1:

Ln (Average Count) = ns (Depth, 3) + Variance: Mean Ratio + Latitude + Gaussian Error

Depth dependence had a clearly non-linear shape and was adequately described by a natural spline function with three degrees of freedom. Average longitude was not significant when the other variables were included. The above model has an R^2 value of 69.2% which implies that most of the variation in the average number of schools recorded in acoustic surveys from Shetland to Senegal can be explained by three simple covariates (Bottom depth, Latitude and the Variance:Mean ratio which measures how fish schools are aggregated). Care was taken to weight the regressions according to the number of observations made during each survey (see N in Table 1). Average school counts are highest at depths of ca 100 m, at high latitudes (60'N) and when schools are most clumped or aggregated in space. This does not mean that you count more schools when there are more schools, but that you actually count more when they are clustered into groups since the variance: mean ratio is independent of the total count. The shapes of these relationships are summarised at three arbitrarily selected latitudes in Figure 14.

Average school S_a per survey

The average school S_a values (Table 2) were also log-transformed and modelled (with a standard linear multiple regression model) as various functions of average bottom depth, distance north (latitude) and distance west (longitude). The following model was selected (Table 2):

Ln (Average S,) = ns (Depth, 2) * Latitude + Longitude + Gaussian Error

Depth was non-linear and was adequately described using a natural spline function with two degrees of freedom. Longitude and latitude were both important. The above model has an R^2 value of 80.5% which is remarkable because it suggests that most of the variation in average pelagic fish school S_a recorded during acoustic surveys from Shetland to Senegal may be explained by reference to two covariates: the interaction between the average bottom depth and distance north (latitude) and the distance east (longitude). The model shows that average fish school S_a increases steadily between average bottom depths of 20-100 m, and that back-scattering energies are greater with increasing distance north and west. The shapes of these relationships are summarised in Figure 15. interaction between latitude and bottom depth is significant statistically and it implies that the shape of the dependence of school S_a on bottom depth changes with latitude which is likely to be true. Nevertheless we have chosen not to explore the effect in detail since its impact on the response variable (average S,) is weak, viz the very slight non-parallelism in Figure 15, and it may also be a result of confounding in the data, which is to say that there is not a full range of average depths covered at average latitudes.

DISCUSSION

The CLUSTER database contains a large quantity of useful biological information which we have attempted to summarise (see Figs l-16) in this paper. The assembly of such a wide-ranging pan-European dataset into a single standardised unit represents a considerable achievement. Nevertheless exposing its scientific secrets in an economic manner is a daunting challenge and this paper describes one out of many possible statistical methodologies which might be adopted.

Section I: Modelling Dependency on Time of Day and Bottom Depth for Each Survey

In Section I school counts and S_a were modelled separately for 39 different surveys as functions of bottom depth and time of day using GAMs incorporating 2-dimensional smooth functions (Beare and McKenzie, 1999b). These allow the shape of the dependency on time of day to be different at different depths, that is to say they allow covariance or interaction between the two predictor variables to be modelled. The results are important from two different perspectives. Firstly they can be considered from a fish behavioural viewpoint. The typical pattern observed in the data is to count more lower energy pelagic fish schools during the mid-day period and fewer higher energy schools at dusk and/or dawn. This behaviour was seen to varying degrees in the Aberdeen, Coruna, Dakar and NW Mediterranean (Part 1) data (Figs 3, 5 and 7) and are due to well-documented patterns of piscean diurnal migration activity (eg Parrish et *al.*, 1964) probably related mostly to feeding and predator avoidance.

At noontime at a given point in space, one typically counts large numbers of small schools. As the day progresses, the schools coalesce into fewer, larger energy (S,) entities. At night the individuals within these schools begin to disperse, probably into shallower water, either as single fish swimming alone, or into much smaller groups that are not resolved as ‘schools’ by the echo-sounding and image analysis equipment (Kieser et *al.*, 1993; Reid et *al.*, 2000). Presumably around dawn these individuals and/or small groups of fish then re-aggregate into relatively few large schools which then further sub-divide into more numerous small schools, typically observed during daylight. [Note: Biases that arise from this type of behaviour underpin the rationale for halting acoustic surveying at dusk and starting again the following morning].

In some instances this typical diurnal pattern of behaviour was not observed. In the Bay of Biscay, fewer, larger schools were seen during daylight in 1991, 1992 and 1994, whereas in 1997 the more typical pattern of numerous, small schools was recorded. We do not know the reason for such apparent changes in schooling behaviour but it does demonstrate the profound range of variability possible in such data. The result might be due to a change in the seasonal timing of spawning or migratory behaviour since it is very unlikely that seasonal effects are constant inter-annually. Our routine visual examination of the Bay of Biscay data indicates that observations were fairly representative over bottom depth, time of day and location, and we felt that it was unlikely that the schooling behaviours observed in the Bay of Biscay were due to confounding.

Secondly, our findings can be considered in the context of fisheries stock assessment. Acoustic surveys are now used routinely for gathering high-resolution spatial information on the abundance of pelagic fish (MacLennan and Simmonds, 1992). As mentioned above, it is common practice to stop surveying at dusk, resuming again at dawn to avoid bias caused by diurnal migration behaviours. It is well documented, (eg Godo and Wespestad, 1993; Petitgas and Levenez, 1996) and also demonstrated here, that pelagic fish are often located at different depths in the water column and have different aggregation patterns (Barange and Hampton, 1997), depending on the time of day.

Unfortunately the present findings demonstrate that this behaviour is in a constant state of dynamic flux throughout the **day,** and that within the daylight portion of the day that is sampled, there nevertheless remains a strongly detectable cyclical signal in the school abundance measurements. The signal, therefore, is not removed by not surveying at night. If sampling activity is random and representative with respect to location, depth, time of day, etc then no serious problems of bias should emerge (Beare and McKenzie, 1999a, b). Consider the May 1997 Heraklion data (see Fig. 16). There are no evening observations in shallow water and it is, therefore, not possible to know if the magnitude of any fish abundance measurement made in deep water in the morning is due to the water being deep or because it is the afternoon.

There are no credible statistical solutions to such severe confounding. An acknowledgement that time of **day** effects should not be ignored, and that such effects are not eliminated completely by discontinuing surveying each dusk, should ensure that future surveys are planned to collect information as randomly and representatively as possible along the axes of all the most important explanatory variables. Admittedly it is not easy to know what these necessarily are at the outset, and it depends on the type of question being asked, but variables of location, depth, and time of day appear to be a very useful starting point for most marine ecological surveys.

Interactions were ‘statistically significant’ in most of the datasets modelled in Section I. This means that the shapes of the diurnal and bottom depth dependencies vary with respect to each other, although few consistent patterns have emerged. Many of the interactions are probably caused by spatial differences in fish species prevalence and age-composition. Unfortunately, for the majority of datasets described here, information on species and age-composition was unavailable and could not, therefore, be considered in our modelling protocols. If such data were available it would, we believe, lead to better fitting models and permit more detailed scientific interpretation,

Section II: Attempting **a** Global **Summary of Fish School Abundance Data From Senegal to Shetland**

In this part of the study the data were summarised using aggregations per survey of a group of key variables (see Tables 1 and 2). The results suggest that average fish school count per survey can be explained by reference to average bottom depth, the total degree of ‘clumping’ by the schools in space and the average distance north (latitude). Similarly, average school size (S,) per survey is acceptably well represented by an interaction between bottom depth and distance north (latitude) and by the distance west (longitude).

Since we have modelled averages of both the response and the predictors, the findings can only be interpreted at that coarse level. Nevertheless, we believe that if some simple information is known about a survey (eg average bottom depth, total mean/variance ratio of the counts, average distance north and average distance west) it is possible to use the models to 'predict' the average school count and S_a values for that survey with a reasonable level of confidence.

Schools from the Aberdeen dataset are all herring, although it is possible that schools are occasionally mis-identified. In all of the other datasets, schools could not be reliably resolved into species and the information is thus unavailable. Fish school size and abundance varies considerably among species (Barange and Hampton, 1997) and this is a cause for concern in both Sections I and II of the present study, and undoubtedly contributes to the variation we failed to explain. Nevertheless the two models described in Section II are so well-fitting, given the variability typical in fisheries data, that they are undoubtedly useful for comparing and contrasting gross school parameters between surveys. If it is imagined that the species of each school are known, then the data would have to be considered to be confounded in space (Barange and Hampton, 1997). There are mainly herring, mackerel and sprats in the north, and sardines and anchovies in the south. Nevertheless, by ignoring the fact that the school abundance and size data comprise multifarious species, we have found parametric models useful for gross, geographic comparative purposes. The models, for example, show that mean fish school count per survey and their mean S_a values are greatest at 100 m depth in the north. Why? We know that the fish in the north are probably mostly herring but the real question is why then do the herring school at higher counts per survey than similar species further south? If we went further north still and included acoustic survey data for capelin, would they then tend to have bigger, more highly clumped schools than herring; and if so why? In a similar vein we can ask why pelagic fish schools are smaller and less clumped or aggregated near the equator, as evidenced by the data collected off the Senegalese coast (Dakar)? Is it because the individual fish are smaller in length; or does some dynamic of the marine tropical ecosystem favour such schooling behaviours as opposed to temperate seas?

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TABLE 1

Summary of School Count Data from 39 surveys from Shetland to Senegal.

Mean count	Variance	Var/Mean	Mean depth (m)	Mean lat	Mean long	N	Survey identification
1.8	13.9	7.7	143.5	59.9	-1.4	2221	Ab July 91
1.2	5.6	4.6	129.1	59.9	-0.9	2234	Ab July 93
2.6	55.1	21.2	129.8	59.9	-1.3	2364	Ab July 94
1.8	9.0	4.9	126.6	60.0	-0.9	2052	Ab July 95
2.5	20.7	8.3	122.7	59.9	-1.4	2140	Ab July 96
2.1	8.9	4.3	123.9	60.1	-1.1	2238	Ab July 97
0.3	0.8	3.0	194.3	43.2	-8.7	750	Coruna April 92
0.6	2.4	3.6	295.7	43.7	-4.8	693	Coruna May 92
0.3	1.4	4.1	280.0	43.5	-7.3	1405	Coruna April 93
0.9	2.6	2.8	230.4	43.5	-2.6	222	Coruna May 93
1.2	4.7	3.8	123.0	43.4	-6.8	542	Coruna May 95
1.0	7.5	7.7	208.9	43.4	-6.7	663	Coruna Mar 96
0.4	1.6	3.8	263.0	43.6	-6.5	1088	Coruna Mar 97
0.3	0.8	2.4	41.2	13.8	-17.2	388	Dakar March 84
0.2	0.4	1.5	46.7	14.5	-17.3	96	Dakar November 84
0.2	0.5	1.9	42.2	14.0	-17.2	482	Dakar December 84
0.3	0.7	2.5	42.8	14.1	-17.2	378	Dakar April 85
0.3	0.9	2.6	42.9	14.0	-17.2	511	Dakar October 85
0.2	0.4	1.9	42.3	14.0	-17.2	442	Dakar February 87
0.4	0.5	1.5	44.2	14.0	-17.2	427	Dakar March 89
0.4	0.8	1.9	43.8	14.0	-17.2	428	Dakar February 92
0.5	1.2	2.6	45.9	14.3	-17.3	187	Dakar March 93
0.5	1.5	3.2	42.1	13.7	-17.2	228	Dakar April 93
2.0	29.9	15.3	61.3	40.1	22.9	519	He October 96
3.7	34.7	9.3	90.4	40.0	23.0	447	He November 97
1.7	6.8	4.0	75.5	45.3	-1.9	652	Bay Biscay April 91
4.4	62.4	14.1	77.3	45.1	-1.8	603	Bay Biscay April 94
0.9	4.0	4.6	75.8	45.4	-2.0	559	Bay Biscay May 95
2.2	12.5	5.6	83.7	45.3	-1.9	677	Bay Biscay May 97

Mean count	Variance	Var/Mean	Mean depth (m)	Mean lat	Mean long	N	Survey identification
0.1	0.1	2.3	112.7	41.7	2.9	232	NW Med(I) October 92
1.2	5.7	4.8	80.8	40.5	1.0	335	NW Med(I) November 92
1.7	12.4	7.3	90.6	41.0	1.7	598	NW Med(I) November 93
1.0	6.5	6.6	87.9	41.0	1.7	582	NW Med(I) November 95
2.3	14.1	6.2	93.2	41.0	1.8	588	NW Med(I) November 96
12.3	95.5	7.8	89.6	43.0	4.0	237	NW Med(II) July 93
10.1	83.0	8.3	71.8	42.8	3.3	70	NW Med(II) July 95
18.2	104.3	5.7	102.9	43.1	4.3	195	NW Med(II) August 95
17.0	226.3	13.3	79.7	43.0	4.0	226	NW Med(II) July 96
16.3	95.2	5.8	84.5	43.0	4.0	177	NW Med(II) July 97

TABLE 2

Summary of School S_a in 38 surveys from Shetland to Senegal

Mean S_a	Variance	Mean depth (m)	Mean lat	Mean long	N	Survey identification
194.83	1.437e+06	133.10	60.11	-0.97	1701	Ab July 91
261.91	1.556e+06	111.94	59.82	-1.25	1428	Ab July 93
201.02	5.742e+06	116.09	59.60	-1.63	1382	Ab July 94
468.64	3.687e+06	124.98	60.00	-1.42	816	Ab July 95
536.88	9.074e+06	127.53	60.03	-1.56	1794	Ab July 96
265.77	6.929e+06	133.78	60.30	-1.32	1862	Ab July 97
154.29	7.208e+04	94.91	42.96	-8.56	177	Coruna April 92
117.35	6.114e+04	97.43	43.58	-4.53	442	Coruna May 92
148.38	8.586e+04	114.81	43.09	-7.41	471	Coruna April 93
99.28	5.089e+04	91.51	43.47	-2.70	192	Coruna May 93
160.72	5.457e+05	103.61	43.35	-6.69	652	Coruna March 96
NA	NA	NA	NA	NA	NA	Coruna March 97
122.88	7.218e+04	102.58	43.61	-4.98	437	Coruna March 97
34.77	1.529e+03	50.93	13.93	-17.22	127	Dakar March 84
27.35	5.030e+02	44.54	14.59	-17.36	23	Dakar November 84
25.77	3.911e+02	40.61	14.11	-17.26	117	Dakar December 84
32.94	5.434e+02	42.57	14.05	-17.22	98	Dakar April 85
20.16	4.326e+02	35.60	13.97	-17.18	166	Dakar October 85
32.62	9.352e+02	63.08	13.92	-17.31	95	Dakar February 87
19.25	7.520e+02	45.82	13.95	-17.20	151	Dakar March 89
23.74	5.330e+02	43.10	14.06	-17.22	171	Dakar February 92
44.42	8.481e+02	68.69	14.38	-17.40	89	Dakar March 93
21.59	5.227e+02	46.97	13.78	-17.16	111	Dakar April 93
24673.2	5.617e+09	27.20	40.25	17.60	1017	He October 96
17625.2	1.649e+09	21.19	40.06	17.64	1668	He May 97
3935.23	1.465e+08	42.33	45.46	-2.48	844	Bay Biscay April 91
3660.95	1.288e+08	37.52	45.07	-2.29	2671	Bay Biscay April 94
4616.74	9.374e+07	40.94	45.31	-2.42	482	Bay Biscay May 95
5035.48	3.328e+08	39.13	45.13	-2.40	1488	Bay Biscay May 97

Mean S_a	Variance	Mean depth (m)	Mean lat	Mean long	N	Survey identification
141.11	4.337e+04	75.22	41.92	2.36	9	NW Med(I) October 92
254.53	2.149e+05	71.35	40.52	0.71	245	NW Med(I) November 92
161.24	5.940e+04	58.15	41.05	1.21	614	NW Med(I) November 93
151.04	7.410e+04	57.18	40.73	0.86	366	NW Med(I) November 95
112.96	4.512e+04	54.70	40.73	0.89	780	NW Med(I) November 96
2123.65	2.152e+07	85.16	43.05	2.87	515	NW Med(II) July 93
3184.39	7.359e+07	66.97	42.84	2.45	141	NW Med(II) July 95
969.77	1.684e+07	94.76	43.11	3.16	1017	NW Med(II) August 95
708.18	1.616e+07	80.42	42.92	2.74	1980	NW Med(II) July96
1011.36	1.412e+07	77.68	42.95	2.80	699	NW Med(II) July 97

FIGURE LEGENDS

Figure 1	Location of CLUSTER Data.
Figure 2	Location of Aberdeen Data, July 1991, 1993-1997
Figure 3.	Dependence of School Count (left panel) and School S_a (right panel) on Time of day and Bottom depth.
Figure 4.	Location of IEO data.
Figure 5.	Iberian Peninsular: Dependence of School Count (left panel) and School S_a (right panel) on Time of day and Bottom depth.
Figure 6.	Location of Dakar Data.
Figure 7	Dakar 1984-1994: Dependence of School Count (left panel) and School S_a (right panel) on Time of day and Bottom depth.
Figure 8.	Location of Heraklion Acoustic Survey Data
Figure 9.	Heraklion and Bay of Biscay: Dependence of School Count (left panel) on School S_a (right panel) on Time of day and Bottom depth.
Figure 10	Nantes: Location of data in the Bay of Biscay.
Figure 11	Location of Data in the NW Mediterranean Sea (Part I)
Figure 12.	Dependence of School Count (left panel) and School Sa (right panel) on Time of day and Bottom depth.
Figure 13	Location of NW Mediterranean Sea (Part II) data
Figure 14	Relationship between Ln(Average School Count), Average Bottom depth, Variance: Mean Ratio and Distance North (Latitude) for 39 Acoustic Surveys from Senegal to Shetland.
Figure 15	Relationship between Ln (Average School S_a), Average Bottom depth, Distance North (Latitude) and Distance West (Longitude) for 33 Acoustic Surveys from Senegal to Shetland.
Figure 16.	Bottom depth vs Time of Day Sampling.

Loca on o Acous c Survey Data used n CLUSTER

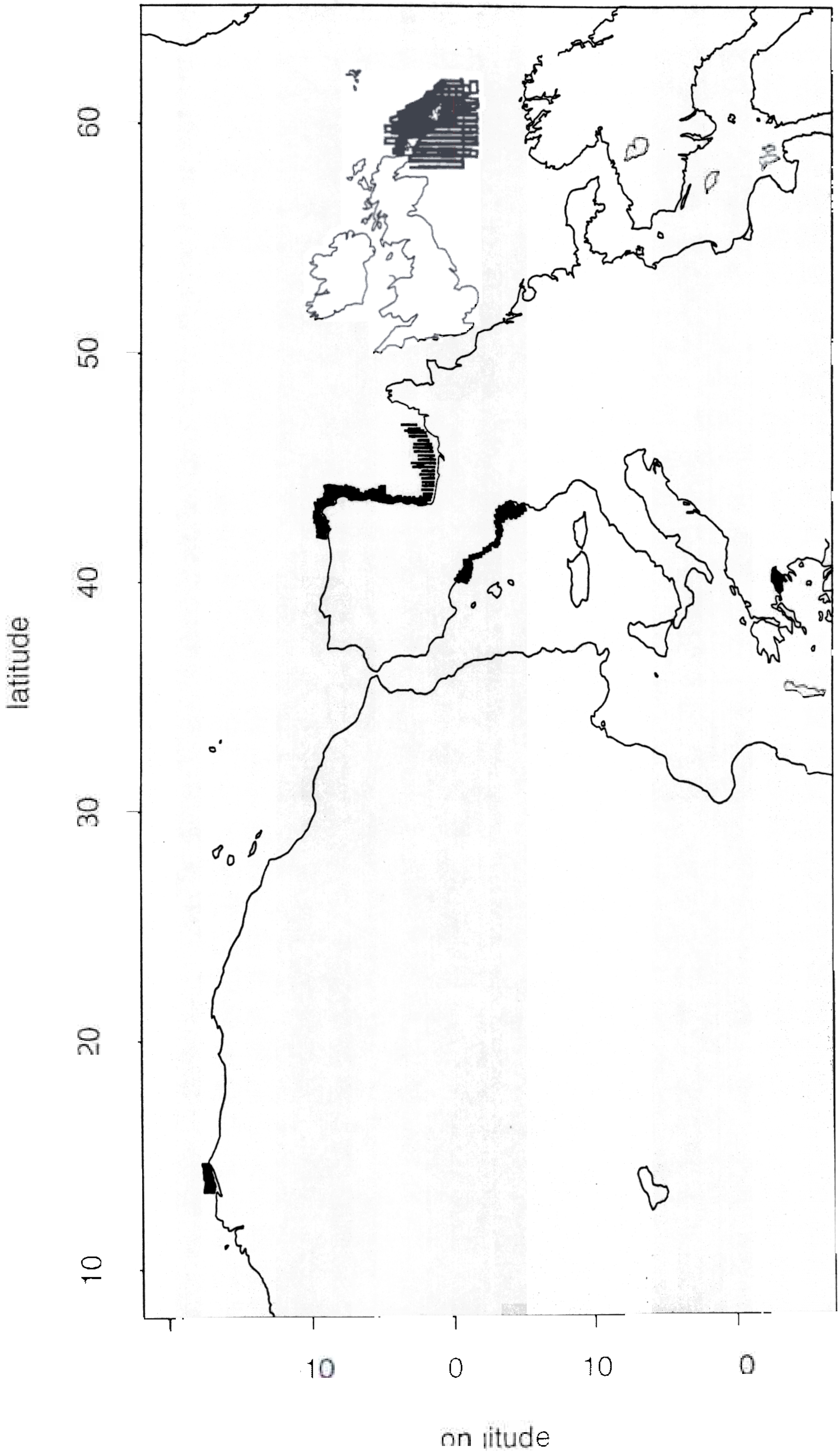


Figure 2

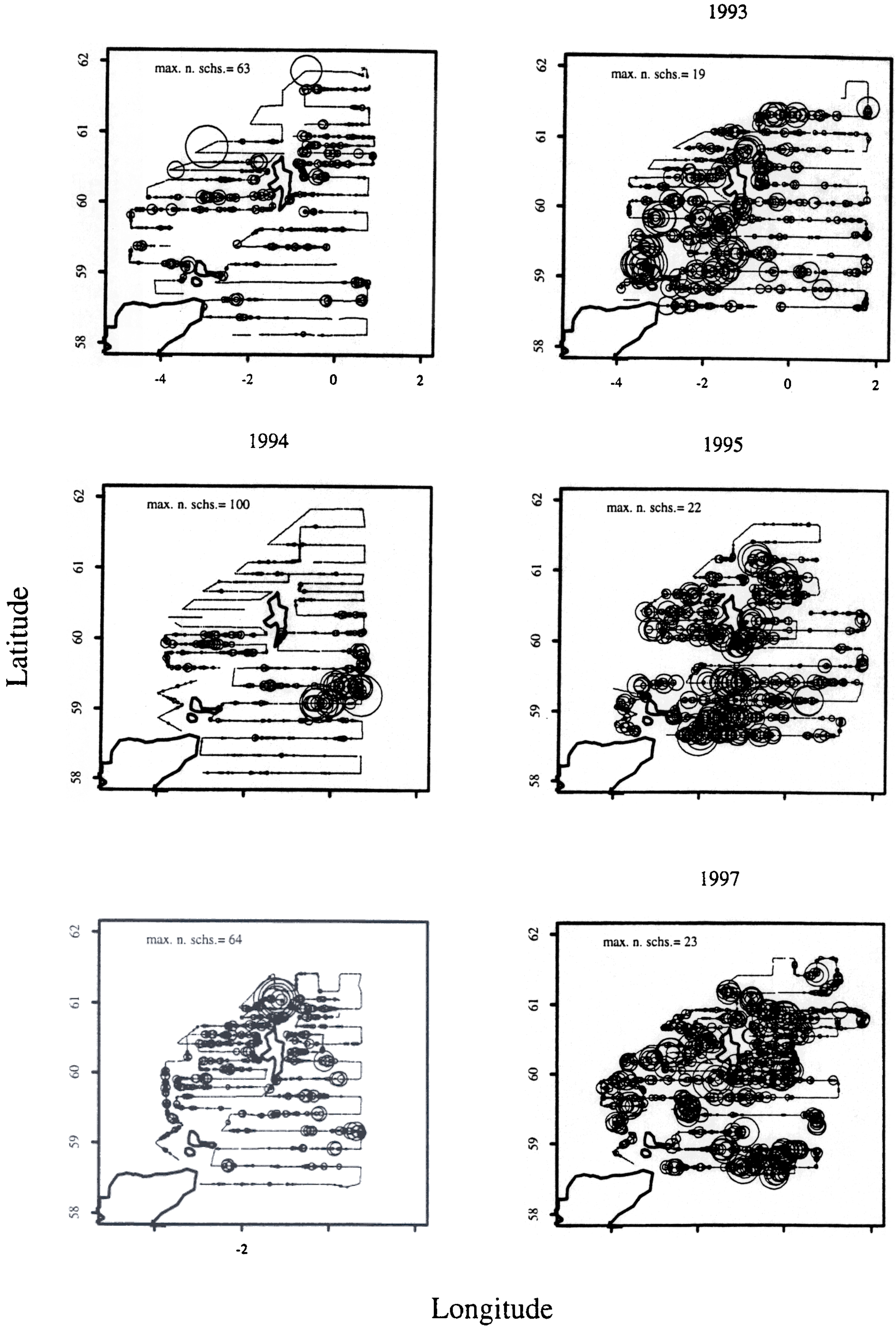

1993
1994
1995
1997
max. n. schs.= 63
max. n. schs.= 19
max. n. schs.= 100
max. n. schs.= 22
max. n. schs.= 64
max. n. schs.= 23
62
61
60
59
58
-4
-2
0
2
Latitude
Longitude

Figure 3

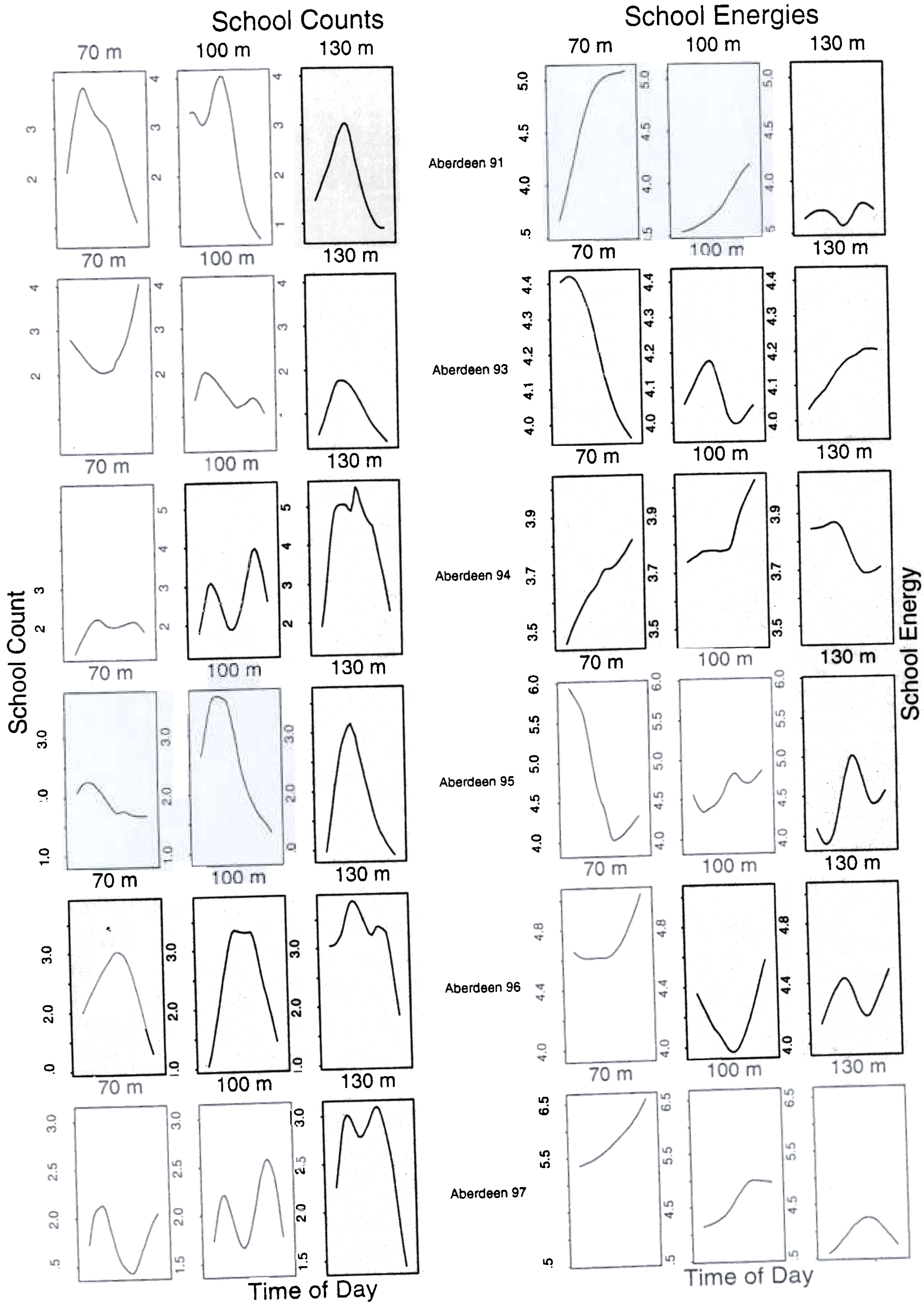

School Counts
School Energies
70 m
100 m
130 m
Aberdeen 91
Aberdeen 93
Aberdeen 94
Aberdeen 95
Aberdeen 96
Aberdeen 97
School Count
School Energy
Time of Day
Time of Day

Figure 4

Coruna Acoustic Data Spring 1991, 1993, 1995-1997

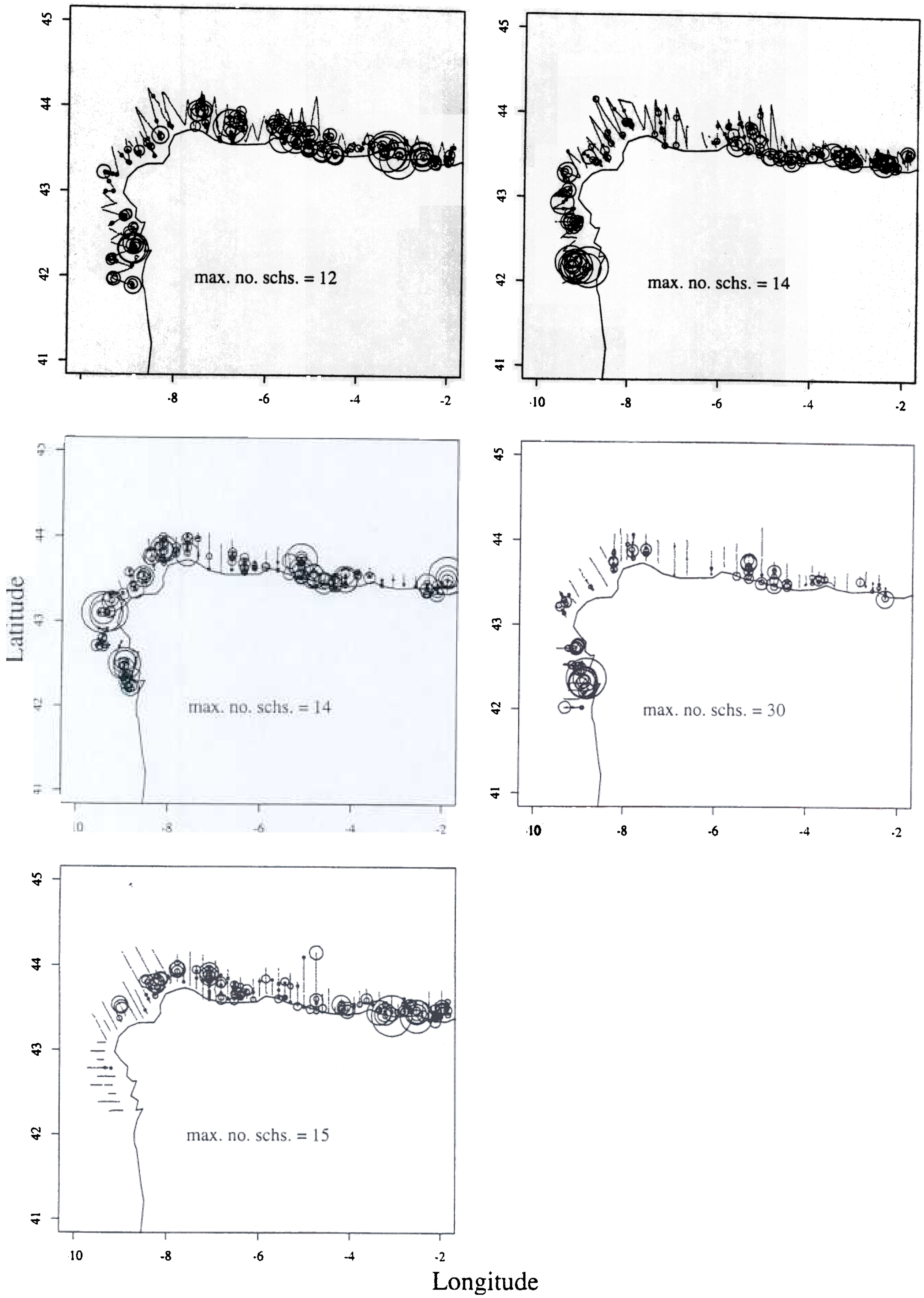


Figure 5

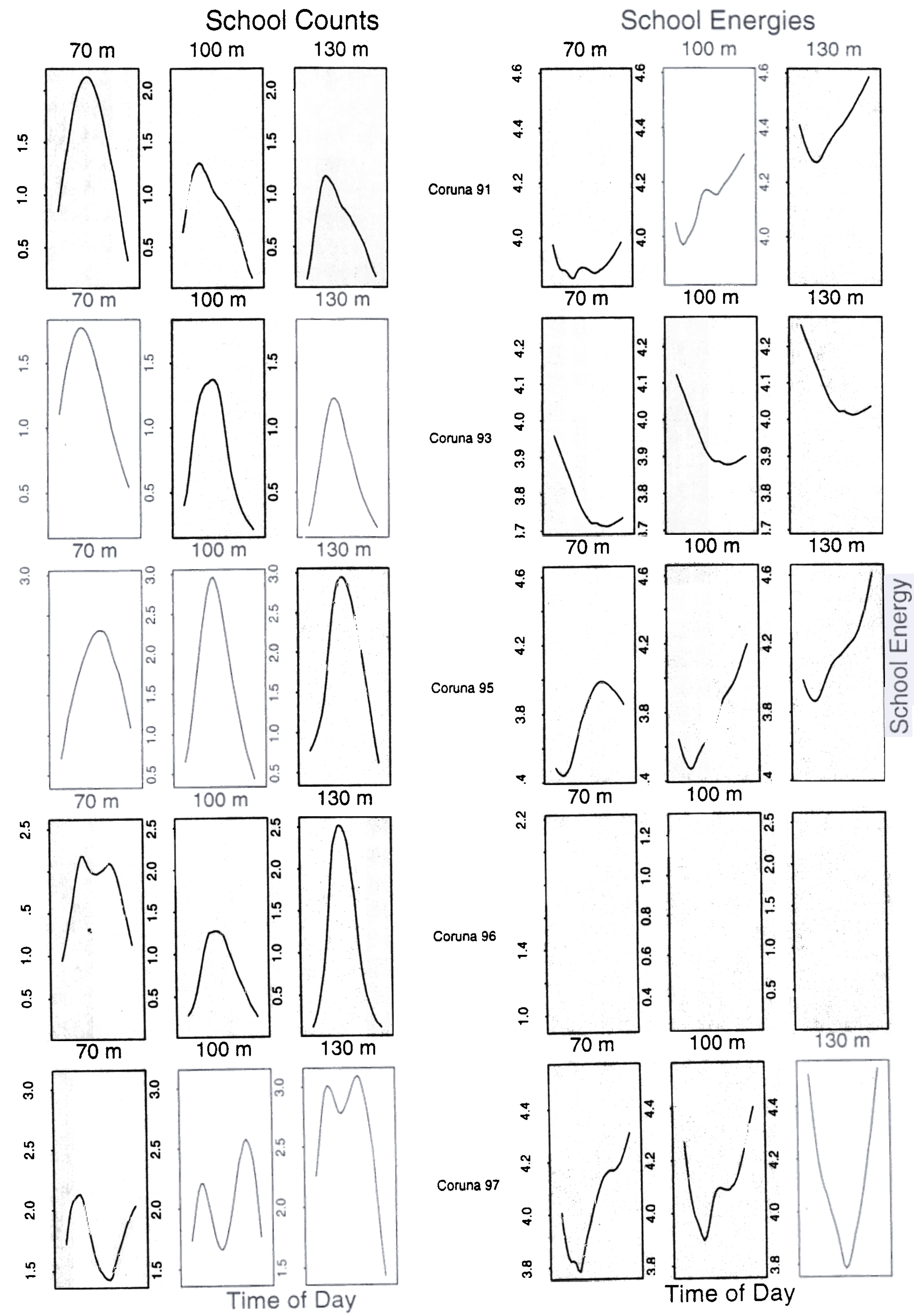
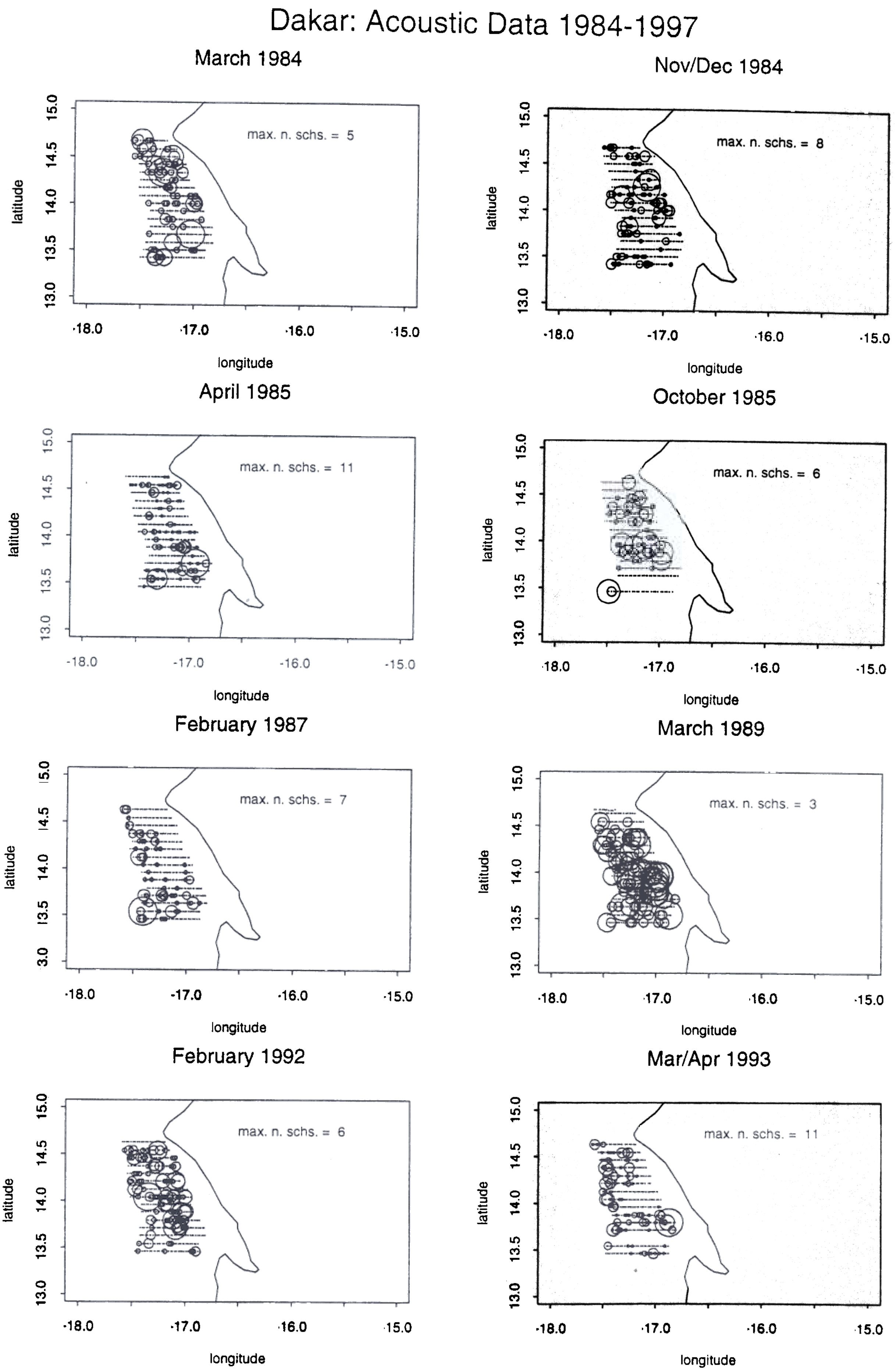
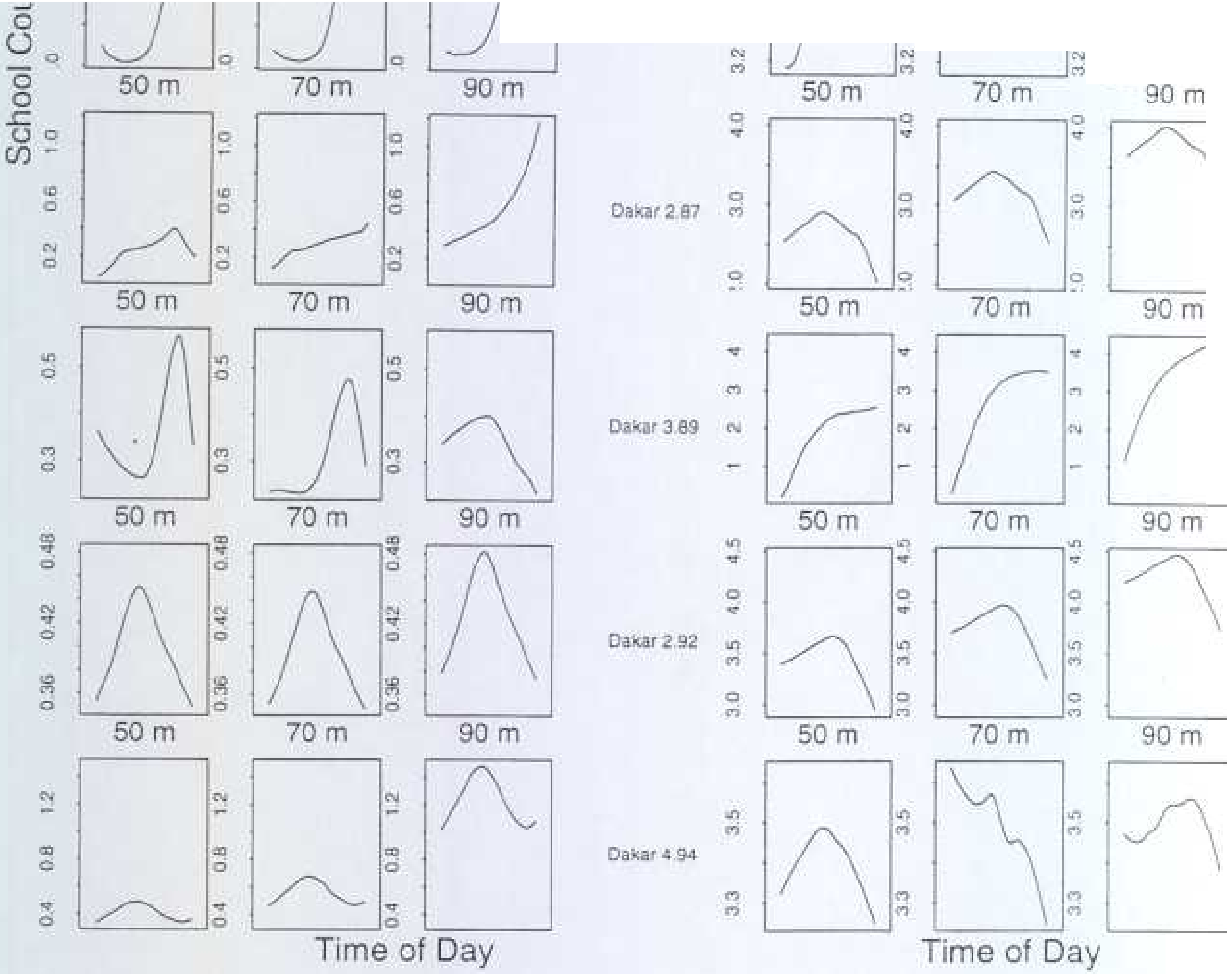
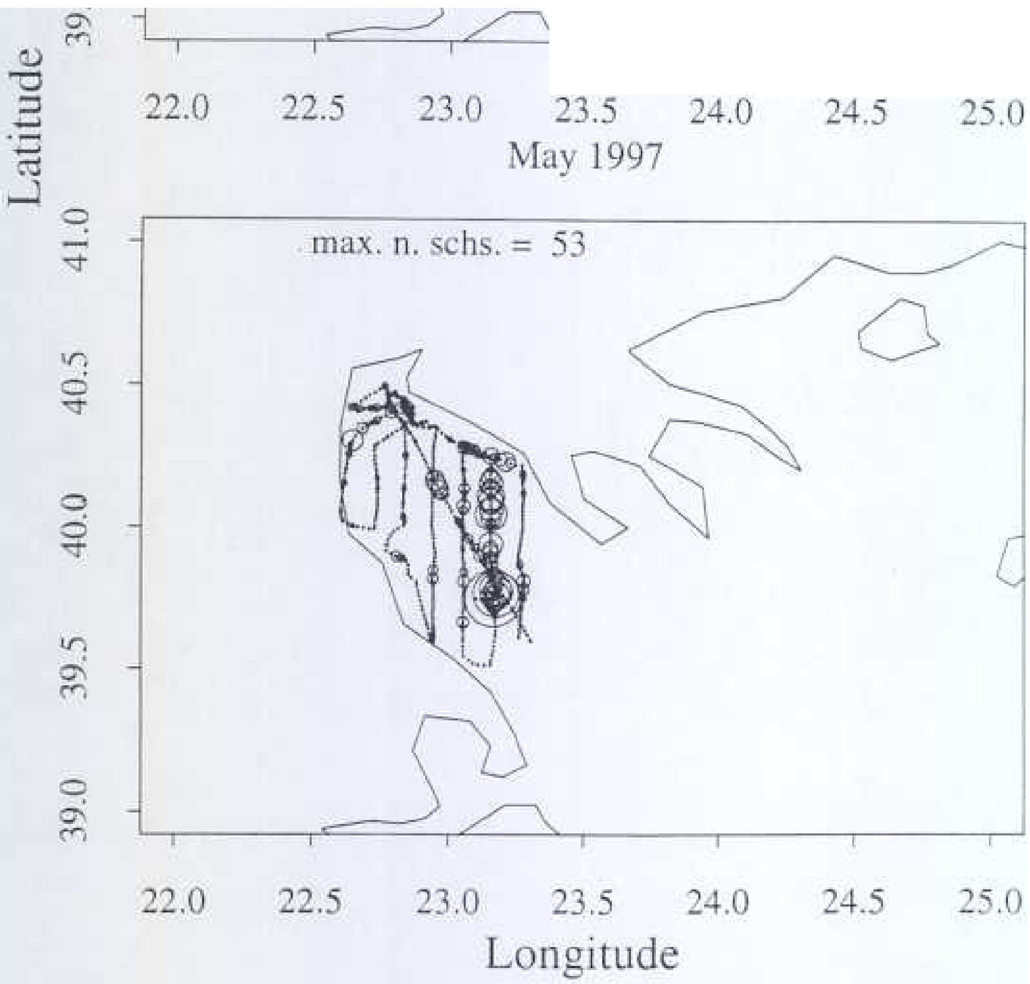

School Counts
School Energies
70 m
100 m
130 m
Coruna 91
Coruna 93
Coruna 95
Coruna 96
Coruna 97
School Energy
Time of Day
Time of Day

Figure 6

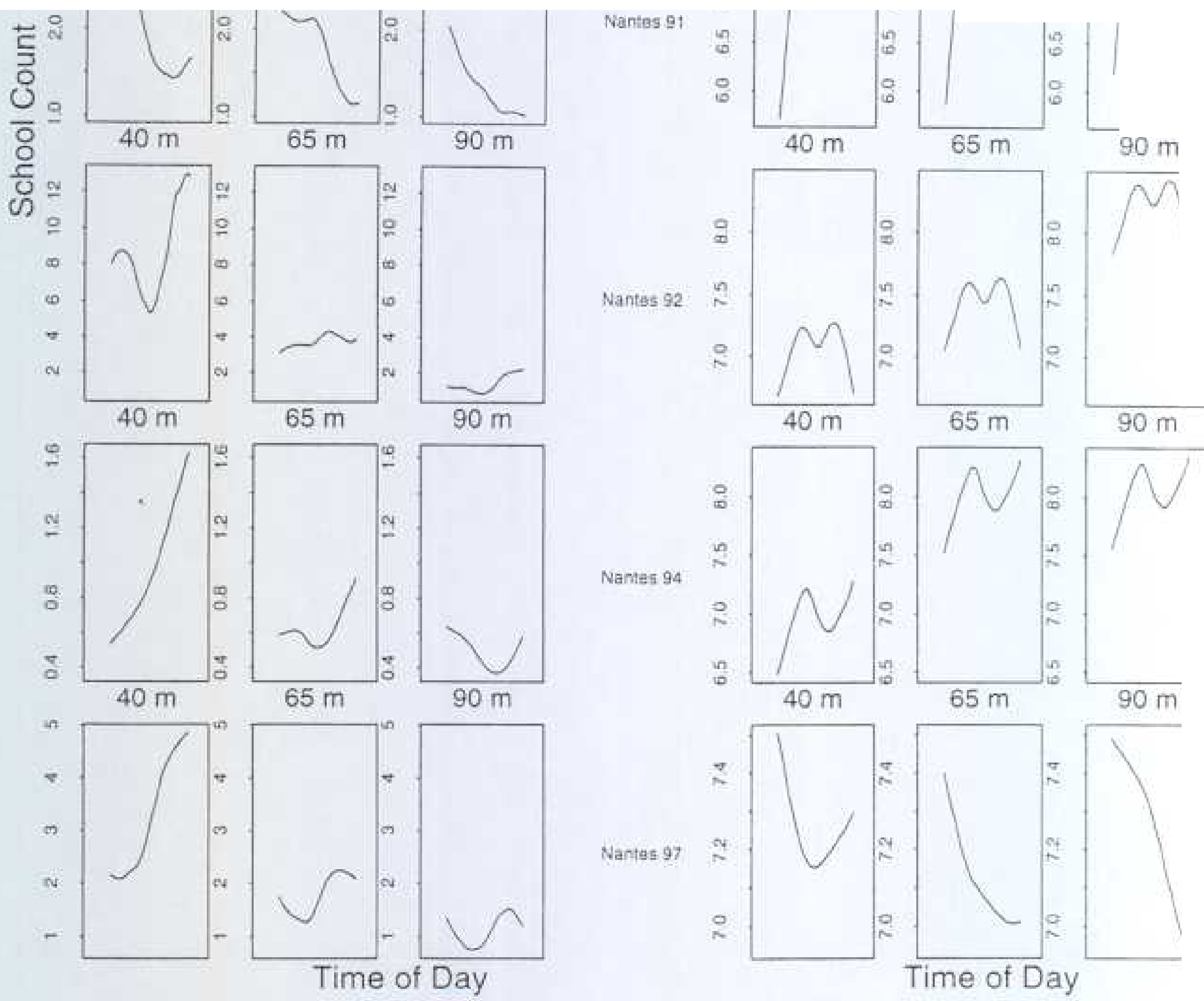

Dakar: Acoustic Data 1984-1997
March 1984
max. n. schs. = 5
Nov/Dec 1984
max. n. schs. = 8
April 1985
max. n. schs. = 11
October 1985
max. n. schs. = 6
February 1987
max. n. schs. = 7
March 1989
max. n. schs. = 3
February 1992
max. n. schs. = 6
Mar/Apr 1993
max. n. schs. = 11
latitude
longitude
13.0
13.5
14.0
14.5
15.0
-18.0
-17.0
-16.0
-15.0

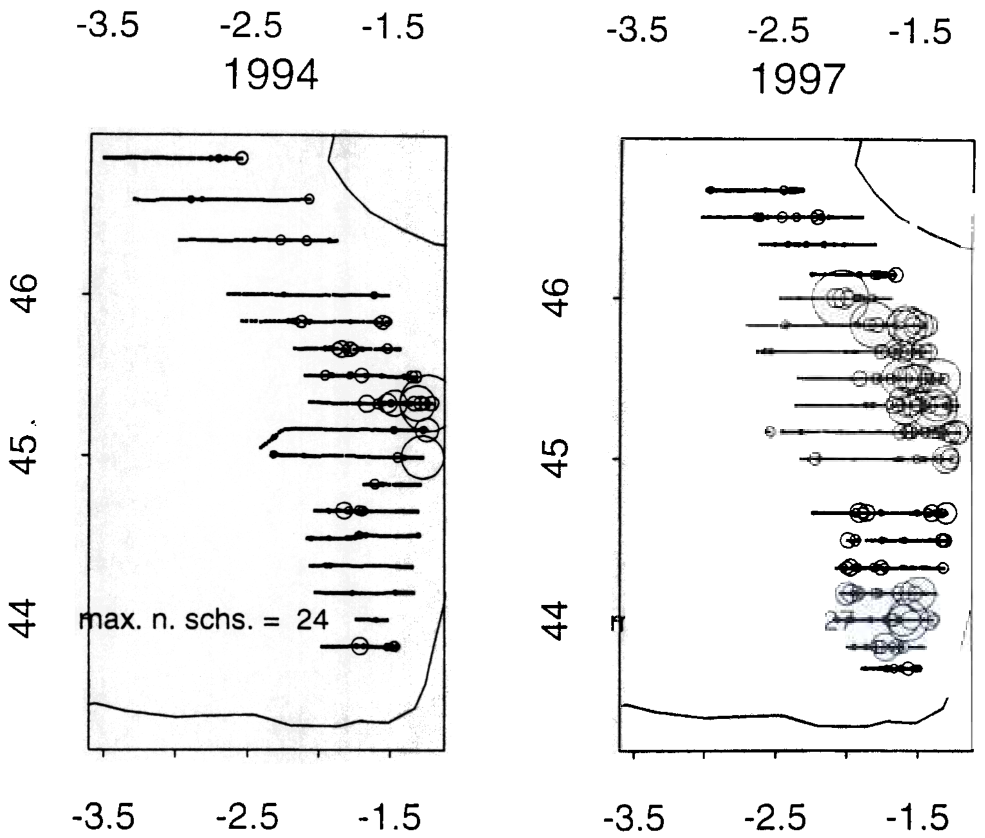


Dakar 2.87
Dakar 3.89
Dakar 2.92
Dakar 4.94
50 m
70 m
90 m
Time of Day
Time of Day

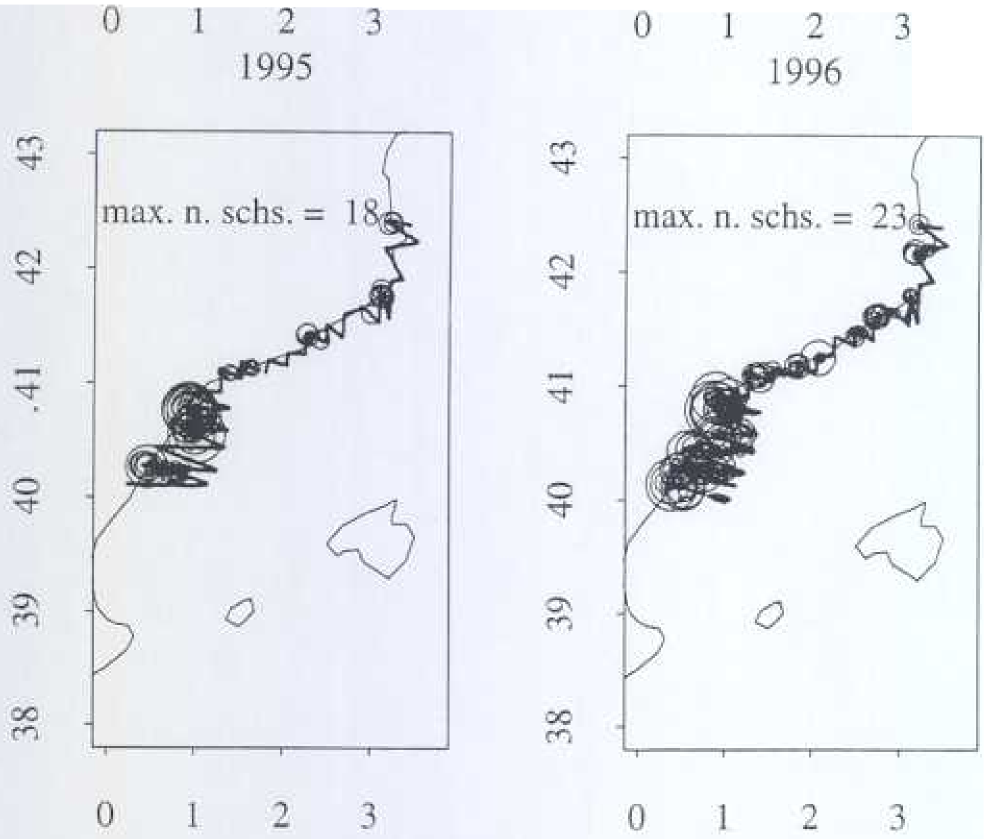


Latitude
22.0
22.5
23.0
23.5
24.0
24.5
25.0
May 1997
max. n. schs. = 53
41.0
40.5
40.0
39.5
39.0
22.0
22.5
23.0
23.5
24.0
24.5
25.0
Longitude


School Count
40 m
65 m
90 m
Nantes 91
Nantes 92
Nantes 94
Nantes 97
Time of Day
Time of Day



1994
1997
-3.5
-2.5
-1.5
46
45
44
max. n. schs. = 24


1995
max. n. schs. = 18
1996
max. n. schs. = 23

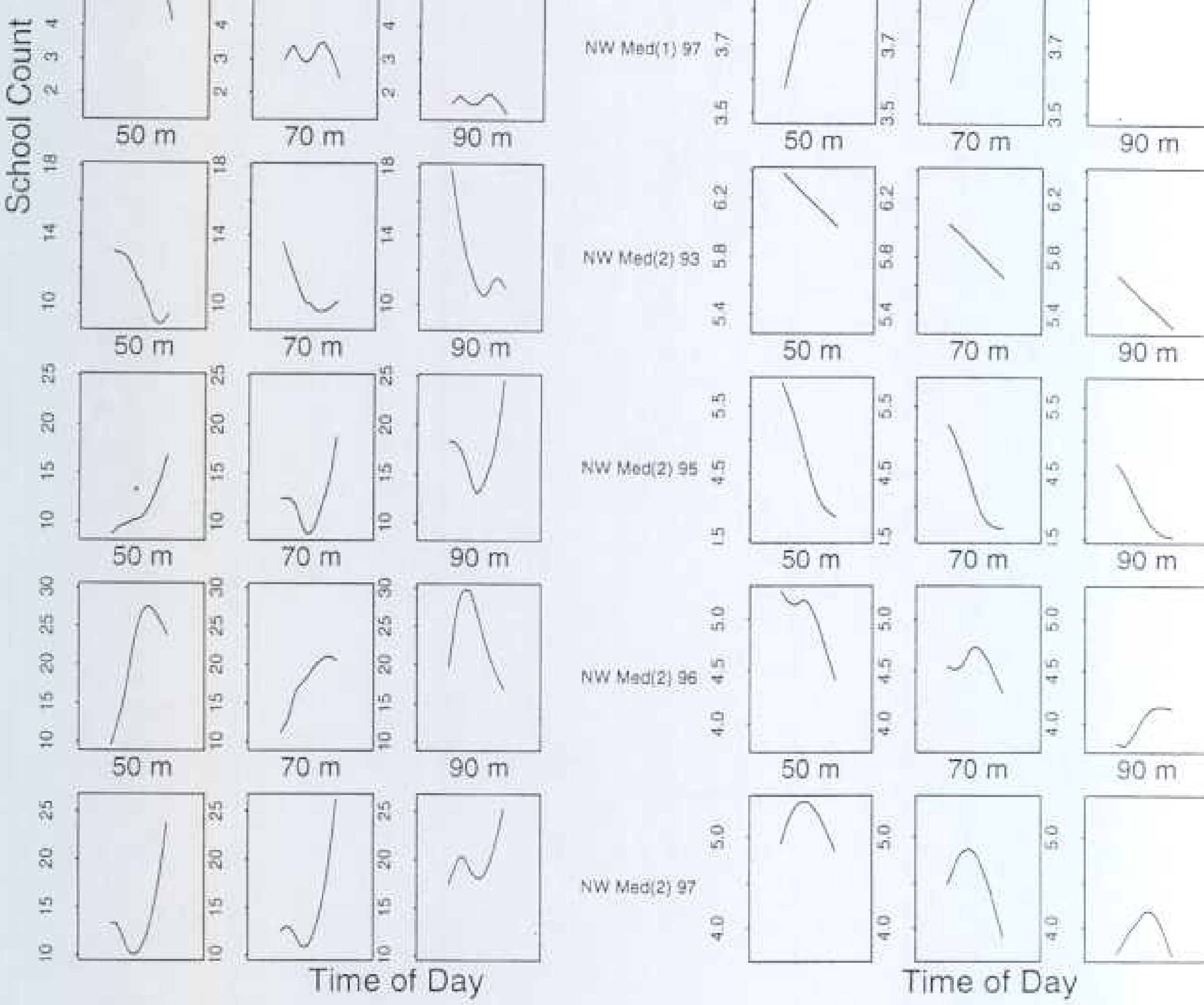
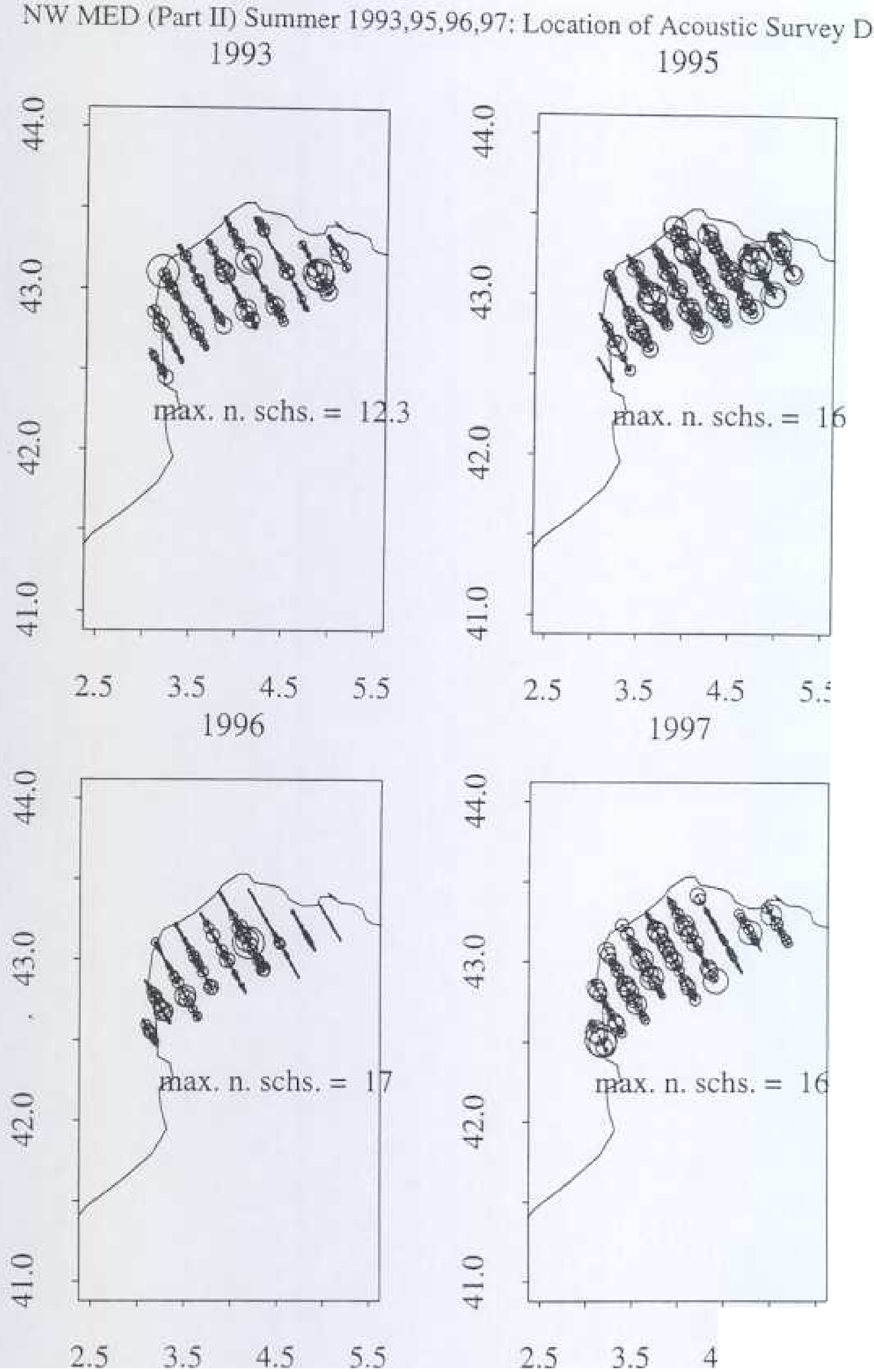
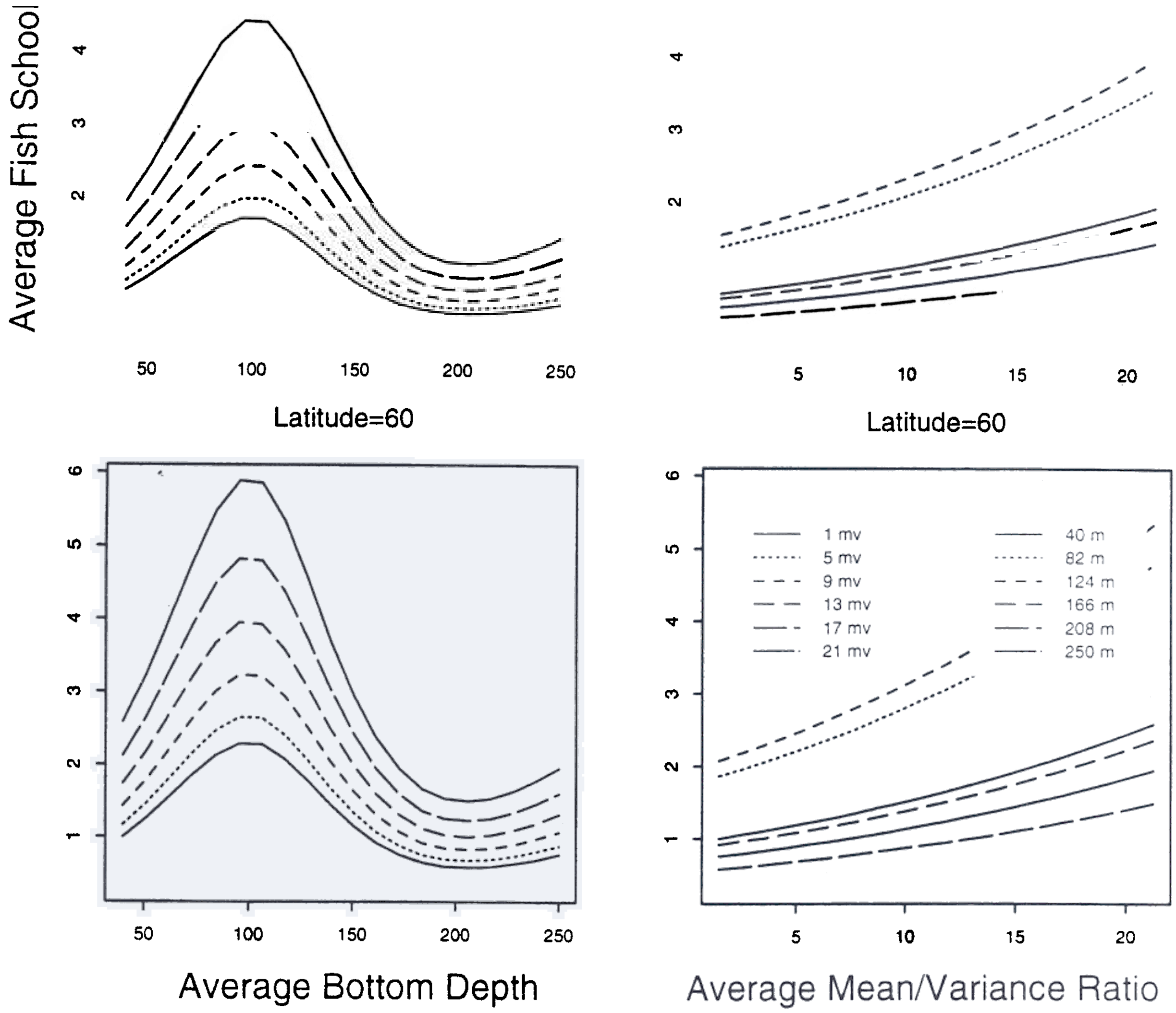
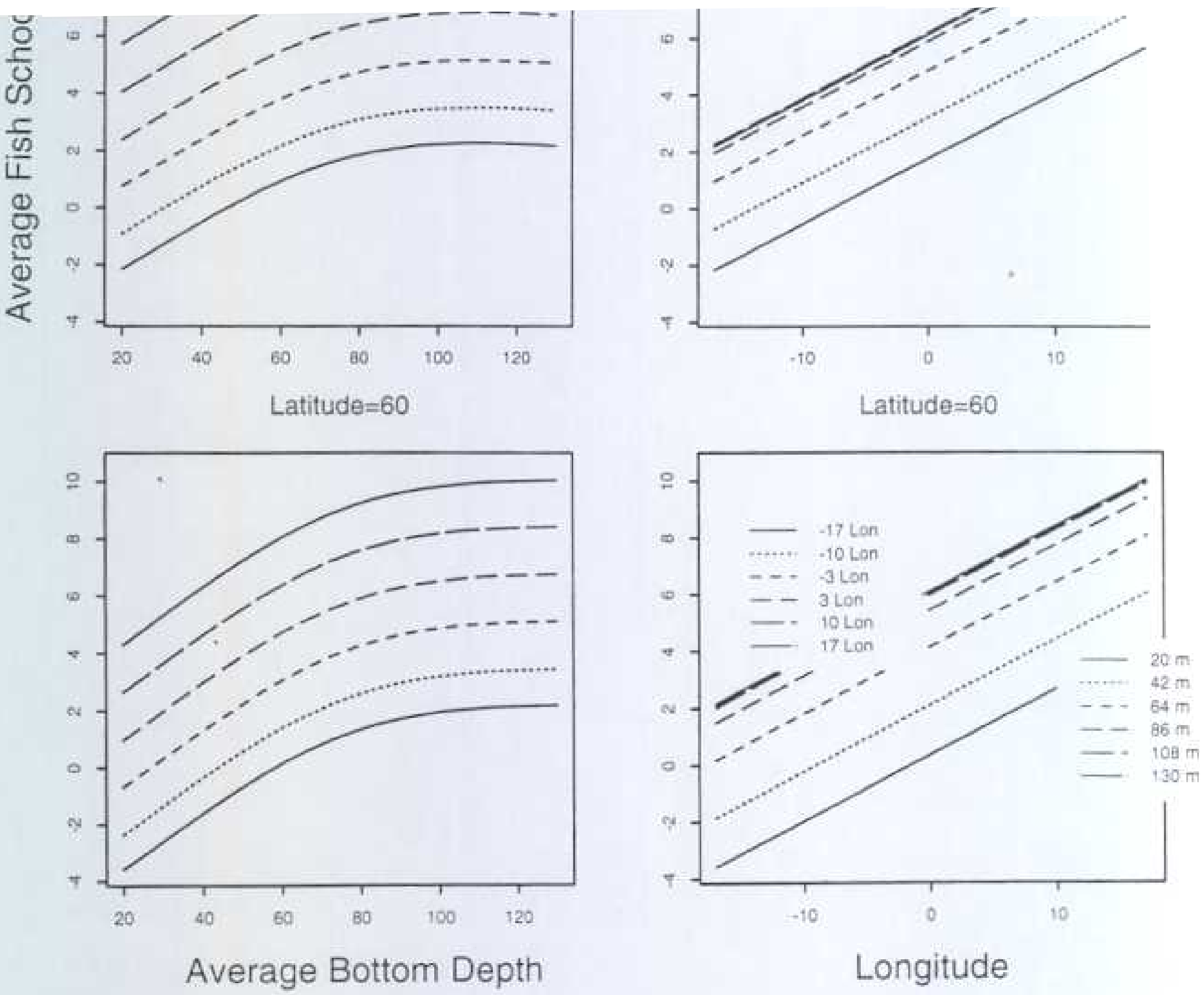
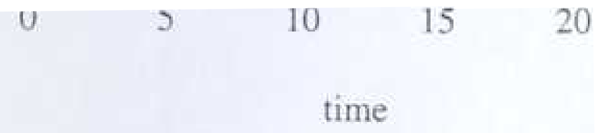

School Count
50 m
70 m
90 m
Time of Day
NW Med(1) 97
NW Med(2) 93
NW Med(2) 95
NW Med(2) 96
NW Med(2) 97
Time of Day

Figure 13


NW MED (Part II) Summer 1993,95,96,97: Location of Acoustic Survey D
1993
1995
1996
1997
max. n. schs. = 12.3
max. n. schs. = 16
max. n. schs. = 17
max. n. schs. = 16
41.0
42.0
43.0
44.0
2.5
3.5
4.5
5.5


Average Fish School
Latitude=60
Latitude=60
1 mv
5 mv
9 mv
13 mv
17 mv
21 mv
40 m
82 m
124 m
166 m
208 m
250 m
Average Bottom Depth
Average Mean/Variance Ratio


Average Fish School
Latitude=60
Latitude=60
-17 Lon
-10 Lon
-3 Lon
3 Lon
10 Lon
17 Lon
20 m
42 m
64 m
86 m
108 m
130 m
Average Bottom Depth
Longitude



May 1997