THEME SESSION (M)

Impact of Cephalopods in the Food Chain and Their Interaction with the Environment

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Relationships between cephalopod abundance and environmental conditions in the Northeast Atlantic and Mediterranean as revealed by GIS

G.J. Pierce, J. Wang, J.M. Bellido, C.M. Waluda, J.-P. Robin, V. Denis, D. Koutsoubas, V. Valavanis and P.R. Boyle

The application of marine GIS, in conjunction with statistical analysis of spatial and temporal patterns, offers the prospect of developing tools for forecasting the distribution and abundance of fished cephalopods. GIS platforms have been established using ARC/INFO software for the Northeast Atlantic and Mediterranean areas. The present paper refers to fisheries in the North Sea, west coast of Scotland, English Channel and eastern Mediterranean. Fishery and survey data on cephalopod abundance, and environmental data (temperature, salinity, bathymetry, sediments, currents etc.) from 1980 onwards have been entered into the system. The GIS systems are now in use to examine spatial and temporal trends in abundance of fished cephalopods in the northern NE Atlantic.

Results are presented on new analyses using the GIS and several different statistical techniques. Correlation analysis on temporal and spatial trends reveals positive relationships between squid *Loligo* abundance (LPUE) and SST in waters around the UK and France, particularly in winter. Identification of areas of similar squid abundance using PCA and cluster analysis, followed by correlation analysis within these areas revealed different relationships between LPUE and SST in the different areas. Finally, preliminary application of GAMs suggests that when seasonal, interannual and geographical effects are removed, peak *Loligo* LPUE is found at temperatures (SST) around 11°C. This analysis is continuing and will examine the role of other environmental and biotic parameters.

Preliminary results from the Mediterranean GIS suggest that cephalopod landings (tonnes) are related to temperature, but the form of the relationship differs between areas. Possible explanations for the spatial variation in catches are discussed.

KEYWORDS: *cephalopods, abundance, GIS, environment, GAM,*

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Introduction

Cephalopod stocks are of increasing economic importance. The value for European landings and exports of cephalopod resources is over 1 billion ECU annually (Globefish, 1994) and recent global trends in fish catch composition appear to show shifts from fish to cephalopod stocks (Caddy, 1995). In this context, there is a need to develop appropriate assessment and forecasting tools.

Cephalopod fisheries show marked inter-annual fluctuations unrelated to fishery catches and effort. Their population dynamics, particularly recruitment, are thought to be strongly susceptible to environmental conditions (e.g. Rodhouse *et al.*, 1992; Pierce, 1995). This arises in part through the short life cycle, resulting in poor buffering of the population against changing conditions. Evidence from Scottish and Portuguese waters supports the general hypothesis that changes in the abundance of *Loligo* spp. may be cyclical (Boyle & Pierce, 1994). Studies on *Loligo forbesi* in Scottish waters demonstrated significant inter-annual changes in abundance and distribution which were strongly correlated with sea temperature and salinity (Pierce, 1995; Pierce *et al.*, 1998). Such correlative relationships are valuable both as the basis for empirical forecasting models and to generate new hypotheses about the underlying causal relationships.

In the NE Atlantic, the UK and France record fishery landings of cephalopods on a monthly catch-by-square (0.5° latitude x 1° longitude) basis, and long time-series of data are available. The information is collected in the same way as that on quota finfish species, and corresponding fishing effort data are also available. Most other European countries collect data on cephalopod landings, albeit usually with a lower spatial resolution, and extensive historical data on the fisheries are available either directly from national Government sources or through international bodies such as ICES or FAO.

Oceanographic, hydrographic and climatological data on appropriate temporal and spatial scales are now available from a variety of sources, including remotely sensed data and outputs from models of air and water circulation, affording an opportunity for detailed examination of the relationships between fisheries and environmental conditions. For example, ICES collates hydrographic survey data in the NE Atlantic. In addition to fishery and oceanographic data, relevant material includes research cruise abundance indices for cephalopods.

Marine GIS has become an important research tool in recent years and systems have recently been developed for cephalopod fishery resources in the SW Atlantic and for the Aegean sea (Mediterranean). The use of GIS coupled with statistical analysis of temporal and spatial patterns represents a particularly important and powerful approach when dealing with short-lived species, known to be susceptible to environmental variation, and for which traditional stock assessment techniques are inappropriate

New work on marine GIS for cephalopod fisheries in the NE Atlantic and the Mediterranean is funded (1997-2000) under a current FAIR project. The main relevant components of this project are:

- development of the GIS: display and overlay of fishery, survey, and environmental data,
- spatial statistical and time-series analysis,
- development of empirical forecasting models,
- testing hypotheses about relationships between cephalopod fisheries and environmental conditions, and generating hypotheses about the underlying causes.

In the present paper we describe the development of the GIS and illustrate preliminary results from analyses of time-series and spatial data on relationships between abundance of fished cephalopod species and environmental conditions.

Development of the GIS for Northeast Atlantic cephalopod fisheries

The cephalopod GIS was developed based on UNIX ARC/INFO v7.11. INFO, Tables, and Arcstorm are used for GIS database. Related databases make use of PC Microsoft Access. The GIS is designed for cephalopod data management, spatial and time-series analysis, modelling, forecasting, and displaying of cephalopod distribution in relation to environmental and biological variates (Figure 1).

The GIS covers the Northeast Atlantic area from 28.0 °W to 11.0 °E, and from 34.5 °N to 65.5 °N (Figure 2). The entire area is divided into 2418 cells (*i.e.*39 rows by 62 columns). Each cell has the area of 1.0 longitude by 0.5 latitude, and is given a unique cell identification number (cell-ID) (Figure 2). The cell-ID is used as a primary key in the database to link different data sets. This spatial resolution was chosen because it corresponds to that of the International Council for the Exploration of the Sea's statistical rectangles. Locations on the grid can be expressed either by ICES rectangle ID or cell ID.

The data collated and integrated into the GIS fall into three catalogues (Figure 1): environmental, fishery and biological data. The environmental data include sea surface temperature (SST), sea bottom temperature (SBT), sea surface salinity (SSS) sea bottom salinity (SBS), currents, sediment, and zooplankton distribution. Fishery data include landings and fishing effort data from national databases in the UK and France, and abundance data from research surveys. Biological data which will be integrated into the GIS include length-frequency, reproductive, morphometric, diet and genetic data on cephalopods, as well as data on the incidence of cephalopods in predator diets.

A geographical coordinate system (*i.e.* longitude and latitude) is used as the basic coordinate system. All spatial data sets are in the same map projection and coordinate system. This facilitates integration of spatial data in the GIS. Coverages are created from different data sets, integrated, overlaid, and visualised together. For example, Figure 3 shows the spatial distribution of total *Loligo forbesi* catch and total effort in relation to sea surface temperature in December of 1993. Figure 4 shows the spatial distribution of total *Loligo forbesi* catch and total effort in relation to sea depth in December of 1989.

To date, most of the analysis has focussed on trends in the abundance of the squids *Loligo* spp., but the approach will be extended to other fished cephalopods.

Correlation analysis of temporal and spatial trends in squid abundance

Pierce (1995) and Pierce & Boyle (submitted) have demonstrated strong correlations between winter and spring temperatures and annual fishery catches of *Loligo* in Scottish waters. A similar analysis has now been completed for squid catches in ICES fishery division VII (Celtic Sea, English Channel and adjacent waters) and is described below (see Robin & Denis, submitted for further details).

We selected rectangles with more than 96 monthly catch and effort values in the period 1989-97. Average LPUE was calculated (total landings/total effort) for each of these rectangles for each fishing year (eight years, each running June-May). Monthly SST for each rectangle was estimated using Météo-France (1° x 1°) grid data.

In each of the selected rectangles correlation coefficients were computed between fishery abundance [LPUE] for the year and temperatures from each calendar month.

The main findings were:

- The highest correlations were observed in the Celtic Sea (sub-divisions VIIg – VIIh), although LPUE was highest in VIIe.
- LPUE was most highly correlated with March temperatures (11 rectangles with significant relationship).
- Negative correlations with LPUE dominated when July SST was used whereas positive correlations dominated when November SST was used.
- There was a clear spatial pattern in relationship of LPUE with temperatures of any month: there was a central area (in the Celtic Sea) with positive correlations while the shelf edge around this area showed negative correlations. The latter result could indicate that squid stay in deeper water in cold winters.

Waluda & Pierce (In Press) used GIS and correlation analysis to test hypotheses on the spatial distribution of *Loligo* spp. in waters around the UK fished by the UK and French demersal fleet (48º - 63º N; 12º W - 10º E). Fishery data (monthly overall LPUE per rectangle, all gears combined, 1989-94) were derived from national databases. Environmental data for this analysis (SST, SBT, SSS, SBS) were provided by the ICES Oceanographic Data Centre. It should be noted that the best coverage for environmental data was in the North Sea. To test the relationship between LPUE and each of the four oceanographic variables, Spearman's rank correlation coefficients were calculated for each month in which data for LPUE and an oceanographic variable coincided in at least 20 grid squares (i.e. the sample size was at least 20). For the purpose of this analysis, each ICES rectangle was treated as an independent data point.

Loligo catches were widely distributed around the UK coast, although distribution and abundance (LPUE) varied from month to month, and between years and was often patchy. The monthly patterns of overall LPUE usually peaks at the end of the year and in at a minimum in June. The area covered by the fishery (1989 to 1994) was relatively consistent and changes in the distribution of LPUE from month to month, which could be interpreted as due to migration, were seen in most of the years studied. From September onwards, there appears to be an influx of squid into the north and south of the North Sea, with the distribution contracting again from January through to July (Figure 5).

Squid LPUE was generally higher in warmer, more saline, waters in the autumn and winter, but these positive relationships tended to disappear in the summer. Of the four physical variables considered, bottom temperature was most strongly related to *Loligo* LPUE, as indicated by the highest number of months with positive correlations. Negative correlations between LPUE and temperature or salinity were most frequent in the summer months (Table 1).

As squid populations tend to consist entirely of a single year group they can be highly responsive to inter-annual fluctuations in biological and physical variables. Population size and distribution patterns can therefore vary widely from year to year (Caddy 1983, Pierce & Guerra 1994, Boyle & Boletzky 1996).

Squid LPUE was highest during October to December, corresponding with the recruitment of young squid to the fishery (Boyle *et al.* 1995). The consistently high abundance of squid in the English Channel may reflect the presence of both species (*L. v. vulgaris* and *L. forbesi*) in this area. The distribution in the northern North Sea contracts during January to April, which could represent northward migration or differential timing of post-spawning mortality.

The four environmental variables examined all tend to co-vary, which suggests that the positive correlation between autumn/winter LPUE and temperature/salinity may be indicate the influence of a given water mass, e.g. the influx of North Atlantic water. Nevertheless, there may be limits to temperature tolerance. Pierce *et al* (1998) found that *Loligo* spp. were absent from survey catches in the North sea in February below a lower limit of approximately 7° C and similar limits are suggested by Holme (1974) for *Loligo forbesi,* Augustyn (1991) for *Loligo vulgaris reynaudii* and Summers (1969) for *Loligo pealei.*

Spatial patterns of squid abundance: application of objective classification methods

Further analysis of the spatial distribution of *Loligo* in relation to SST has made use of the same LPUE data set (although extended include 156 months from 1982-1994). However, for SST, we used monthly averaged sea surface temperatures retrieved from NCAR (National Center for Atmospheric Research), USA. The NCAR SST data are global and recorded by 1.0° longitude and 1.0° latitude. The SST subset for the Northeast Atlantic was re-sampled to give values for each GIS grid square (1.0° longitude by 0.5° latitude).

The statistical package S-PLUS was used for spatial analysis. The LPUE values for each of the 156 months were treated as separate variables and the dimensionality of this data set reduced by application of PCA. The first 5 principle components, which together explain over 90% of all the variance of the original data, were selected for spatial classification. Cluster analysis was then used to define areas of similar LPUE. Five classes of LPUE were thus defined, levels 1-5. The areas characterised by these levels of LPUE are henceforth referred to as areas 1-5 (Figure 6). Of these, area 1 has very low LPUE and shows relatively little seasonal variation in LPUE and (although it covers a wide area) was not used in further analysis. Areas 4 and 5 were also excluded since both have very limited and isolated spatial distribution in Northeast Atlantic (Figure 6).

Area 2 is mainly along the French coast, around the Scilly Isles (southwest England), in the Irish Sea, and on the Northeast Scottish coast. Area 3 is mainly along the southern part of the French Atlantic coast, in the English Channel (excluding the French coast) and off northern Scotland. Seasonal trends in LPUE are similar in both areas, although LPUE is higher in area 3 and the seasonal peak is reached one month later (November, as compared to October in area 2; Figure 7).

Correlations between monthly *Loligo* LPUE and SST were calculated separately for areas 2 and 3 (Tables 2, 3). Monthly averages (averaged across all years) were derived for both SST and LPUE prior to correlation analysis. In area 2, the LPUE in the first half of the year was strongly positively correlated with SST, but LPUE in August to December was weakly or negatively related to SST. In contrast, in area 3, LPUE in July to October was strongly positively correlated with SST. For LPUE in other months, while relationships with SST were weak or negative. Some of these relationships are illustrated in Figures 8-10.

In area 2, when SST is below 15° C in August, May LPUE remains low, but at high temperatures, LPUE increases with SST (Figure 8a). April LPUE and October SST show a similar relationship in area 2 (Figure 9a). In contrast, in area 3, a negative relationships is seen between April LPUE and October SST (Figure 9b). Similarly, areas 2 and 3 differ with respect to the relationship between September LPUE and April SST: in area 2 the relationship is weakly negative (Figure 10a) whereas in are 3 the relationship is positive below 10°C and negative at higher temperatures (Figure 10b).

Although these results broadly confirm previously established positive relationships between squid abundance and temperature, particularly in the winter months, they reveal a more complex structure in the data, which, at present, is difficult to interpret.

Other environmental factors (e.g. currents, sea bottom temperature, salinity, sediments) and biological variables (e.g. genetic variation, prey distribution) could have more effect on squid distribution than SST in a particular area, and help to answer questions such as why areas 2 and 3 show such different relationships between LPUE and temperature. Further investigation is in progress to study the relationships between squid distribution and other environmental and biological variables.

Application of general additive models to the analysis of squid distribution

Generalised additive models (GAMs, S-PLUS software) were used to model trends in *Loligo* abundance as functions of geographical position and environmental variables with the main aim being to draw inferences about the mechanisms that give rise to the distribution of squid.

A generalised additive model is a generalisation of the linear regression model. The central idea is to replace the usual linear function of a covariate with a specified smooth function. The additive model consists of a sum of such functions. Hastie and Tibshirani (1990) give a detailed explanation of GAMs.

Input data for the models were longitude, latitude, month, SST, and LPUE. LPUE data (monthly, per statistical rectangle) were as described above for UK waters, although the present analysis is restricted to three years (1988, 1991 and 1995), chosen to assess the reliability of the model. Monthly SST data were accessed from NCAR.

The preliminary models presented here used LPUE as the dependent variable. The independent variables considered were month, SST, latitude and longitude. This analysis includes both spatial and temporal components. Month was included to remove the effect of seasonal differences in abundance and interannual differences are excluded by considering data from each year separately. Cubic spline smoothers (Hamming, 1973) were used in the GAM model. Results are shown in Table 4 and Figures 11-13.

The plots show the best fitting smoothers (and 90% confidence limits) for the effect of the covariates month and SST on the parameter of interest, i.e. squid abundance (LPUE). The x-axis for the single covariate effect plots includes a so-called "rug", which shows the density of points for each covariate included in the model. The y-axis reflects the relative importance of each covariate in the model.

Interaction effects of longitude and latitude for the months of June and December of each year are also presented, as perspective plots without error bounds. These months represent the periods of lowest and highest abundance indices. For the interaction effects the relative importance of the covariate appears on the z-axis.

It needs to be emphasised that the effect of each variable shown in the figures is the conditional effect; that is, the effect of this variable has given that the other variables are included in the model.

Studies in Scottish waters have demonstrated significant inter-annual changes in abundance and distribution, strongly correlated with SST and salinity (Pierce, 1995; Pierce *et al.*, 1998). The present analysis also suggests a clear relationship between LPUE and SST, with the highest LPUE at temperatures of around 11° C. As expected from previous work, the highest LPUE was found in winter months.

The three-dimensional plots showing the spatial pattern of LPUE (Figures 11-13 c for June and 11-13d for December) show that spatial effects on squid abundance are higher in December than in June, and that LPUE is generally higher to the west.

Cephalopod distribution in relation to environmental conditions and fishing methods in the Eastern Mediterranean (Greek Seas)

In parallel with work in the NE Atlantic, a GIS for the eastern Mediterranean is being extended to include information on cephalopods. The Cephalopod GIS database is under development and extensive checking of the values is currently being performed. The present paper presents data from 1997. All data are part of the Cephalopod Marine Information System (CMIS) for Greek Seas, which also includes bathymetry and SeaWiFS data.

SST data for 1997 were obtained from Deutsches Zentrum fur Luft und Raumfahrt (DLR), Germany (monthly means with a spatial resolution of 1.6 x 1.6 Km). These data were processed using the ESRI ARC/INFO GRID module in UTM projection.

Cephalopod landings data were obtained from IMBC. They are monthly total landings of all fished cephalopods, by 80 x 80 km square and by gear. The main fished species are long-finned squid (*Loligo vulgaris*), short-finned squids (*Illex coindetii, Todarodes sagittatus*), cuttlefish (*Sepia officinalis*), common octopus (*Octopus vulgaris*) and musky octopus (*Eledone moschata, Eledone cirrhosa*). Data on fishing effort (by gear) were also obtained from IMBC and have the same spatial and temporal resolution as the landing data. These two data sets were processed using the ESRI ARC/INFO ARCEDIT and ARCPLOT modules.

In the 1997 Cephalopod fishing season, production was generally lowest in June to September (when SST is high). There was a drop in the fishing activity during this period mainly due to the fact that demersal trawl fishing (the main gear type for the collection of the majority of Cephalopod species) was prohibited by Greek fishing regulations. The fall in landings may also be related to the recruitment period of the species in question (generally in summer and autumn).

The geographical variation in cephalopod landings in Greek Seas may be attributed to two main factors:

1. The eutrophic character of the North Aegean Sea due to large riverine input in contrast with the oligotrophic character of the South Aegean and Cretan Seas. The North and Central Aegean Seas are characterized by primary landings one order of magnitute higher than those from the South Aegean, Cretan, and Ionian Seas.

2. The extented continental shelf in the North Aegean Sea.

In the North and Central Aegean Sea, which are affected by the colder Black Sea waters, and in the Ionian Sea, which is indirectly affected by the colder Atlantic and Eastern Mediterranean deep waters, landing peaks occur when SST is around 18° C. In contrast, in the South Aegean and Cretan Seas, which are affected by the Levantine intermediate water, landing peaks occur at around 22° C.

Conclusions

The development of marine GIS for cephalopod fisheries allows integration and management fishery, survey, biological and environmental data. It also facilitates the analysis, modellin, and visualisation of spatial and temporal trends in distribution and abundance of cephalopod in relation to environmental conditions. Ultimately it can produce a forecasting tool for use in fishery management.

The present results show that squid (*Loligo* spp.) abundance is related to SST in both the Northeast Atlantic and the Mediterranean. We have carried out a series of different analyses which reveal different aspects of the relationship between temperature and abundance and not all of which are currently interpretable. The mechanism by which SST might be related to LPUE is not clear: Waluda & Pierce (In Press) discuss several alternative mechanisms involving both direct and indirect relationships. Further work will explore the role of other environmental and biological variables that may also influence squid distribution and abundance. We will also extend the analysis to other fished cephalopod species.

Acknowledgements

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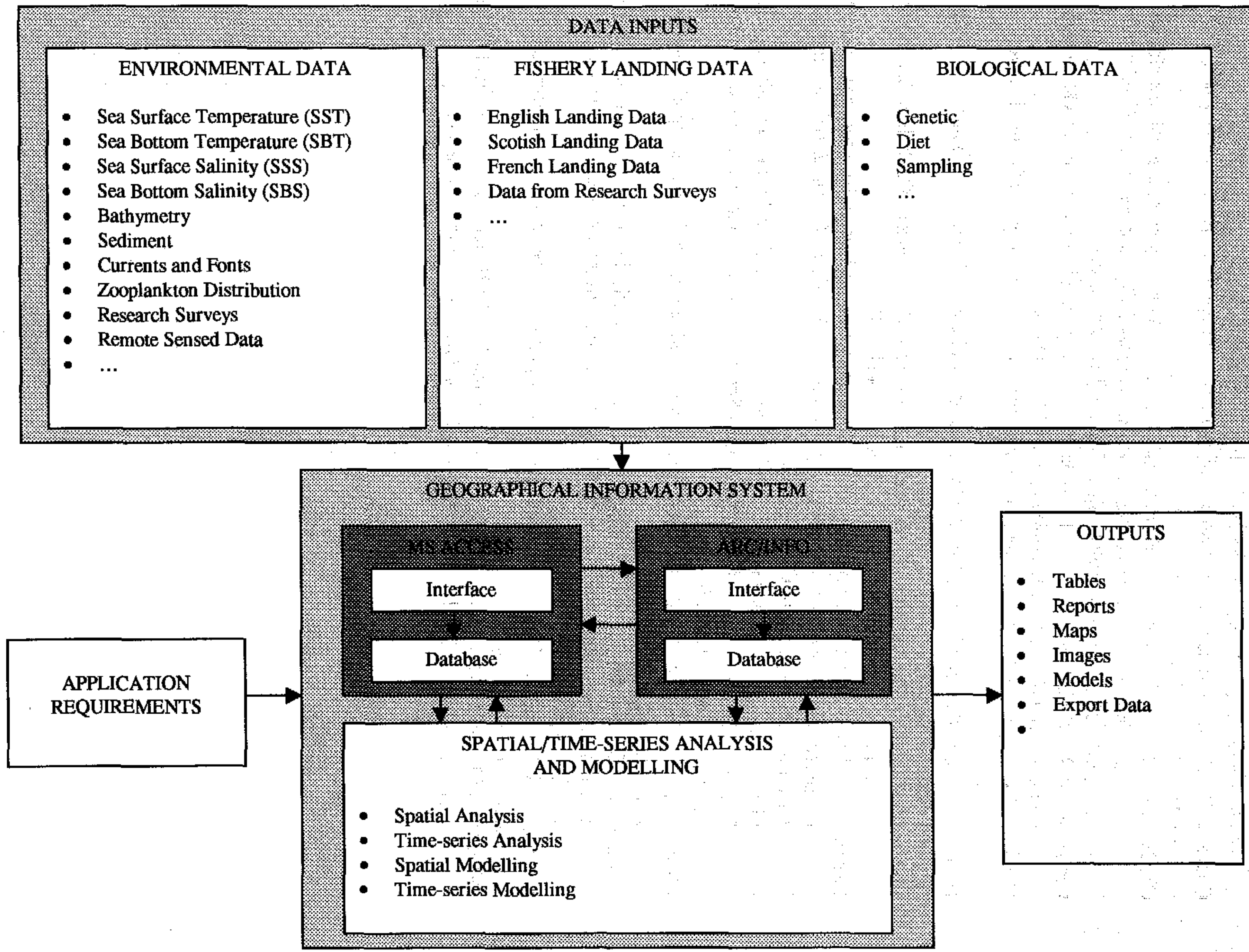


Figure 1: The structure of the cephalopod GIS.

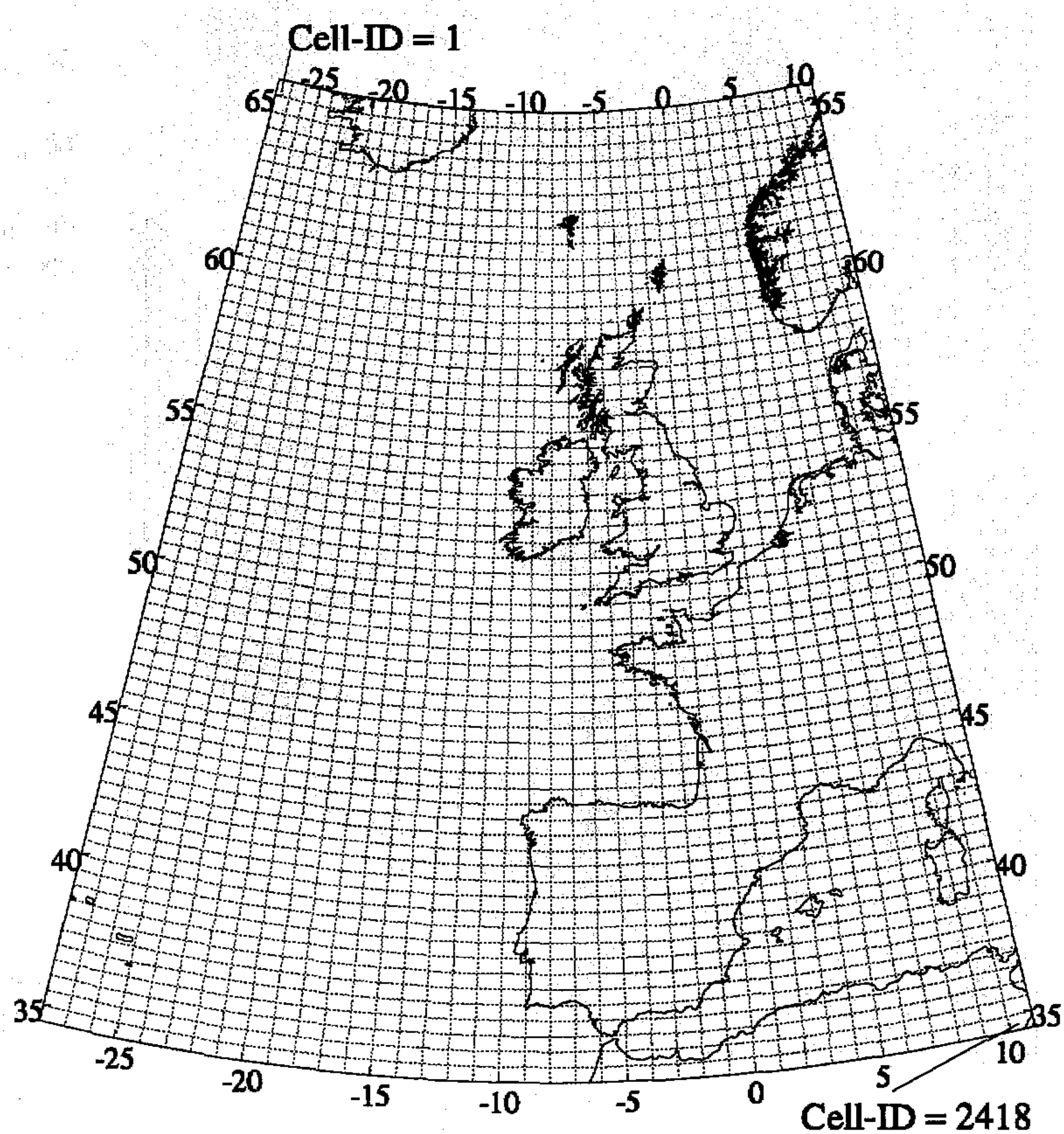


Figure 2: The Northeast Atlantic area covered by the Cephalopod GIS. It is divided into 2418 cells.

SQUID CATCH IN RELATION TO SEA SURFACE TEMPERATURE: 12/93

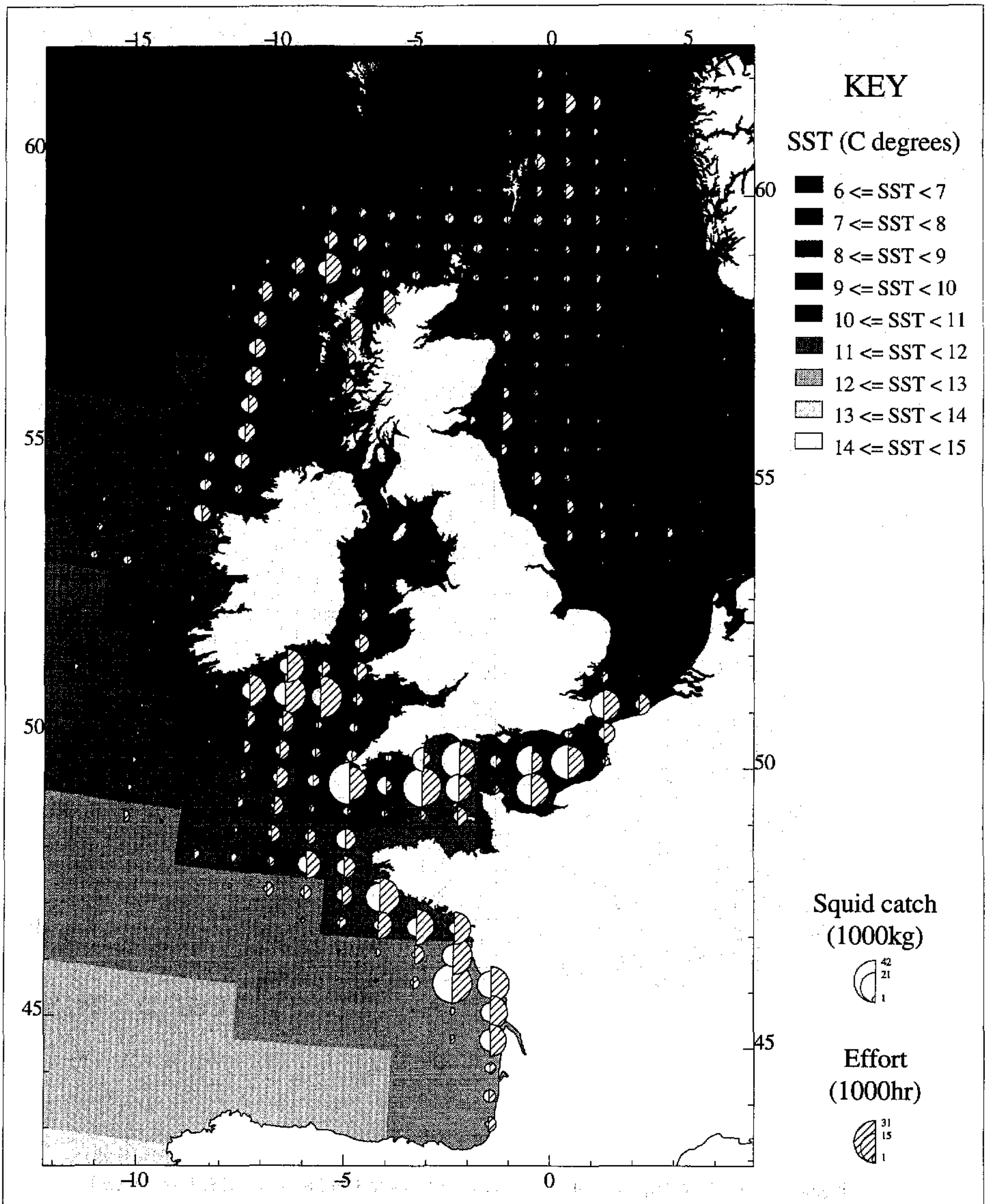


Figure 3: Spatial distribution of total *Loligo forbesi* catch and total effort in relation to sea surface temperature in December of 1993.

SQUID CATCH IN RELATION TO SEA DEPTH: 12/89

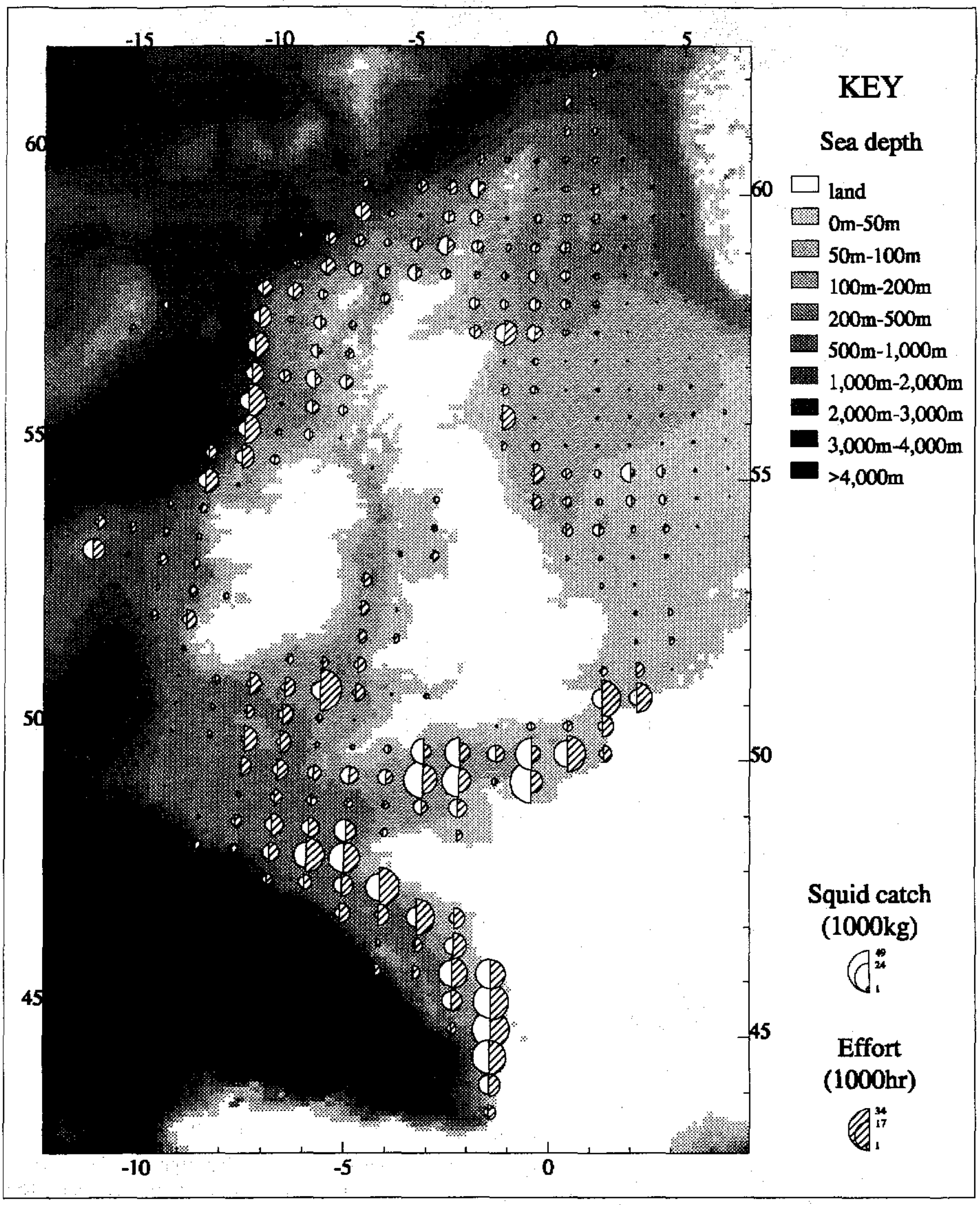


Figure 4: Spatial distribution of total *Loligo forbesi* catch and total effort in relation to sea depth in December of 1989.

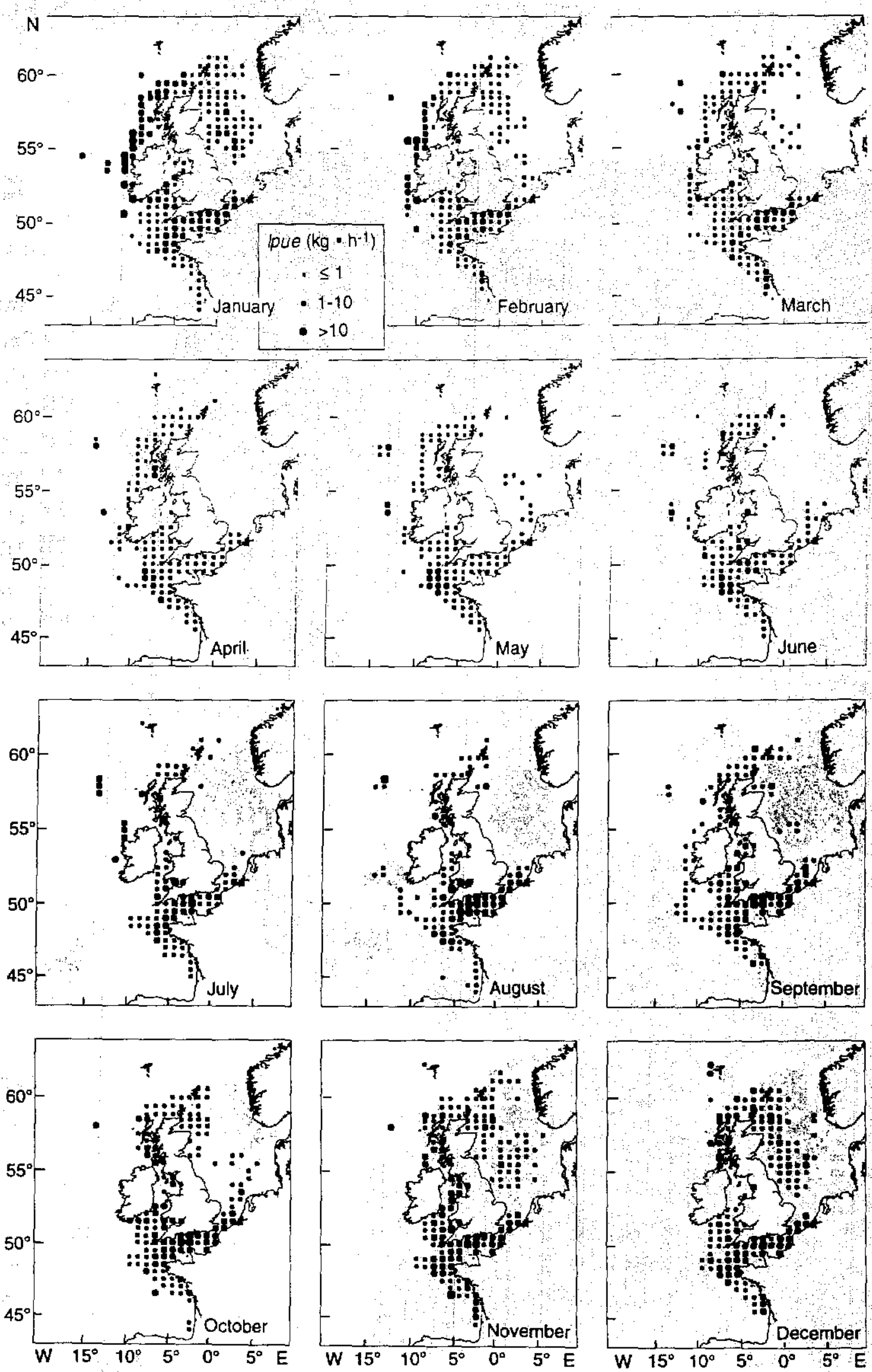


Figure 5: Squid (*Loligo* spp.) distribution and abundance, 1994. Circles represent landings per unit effort (LPUE [kg hr^{-1}]). Shaded areas represent areas in which fishing (demersal fleet) took place. *Loligo* are widely distributed over the entire region between September and December, but restricted to waters in the North West and English Channel between January and August.

SPATIAL CLASSIFICATION OF SQUID LPUE (Kg/Hr) DISTRIBUTION

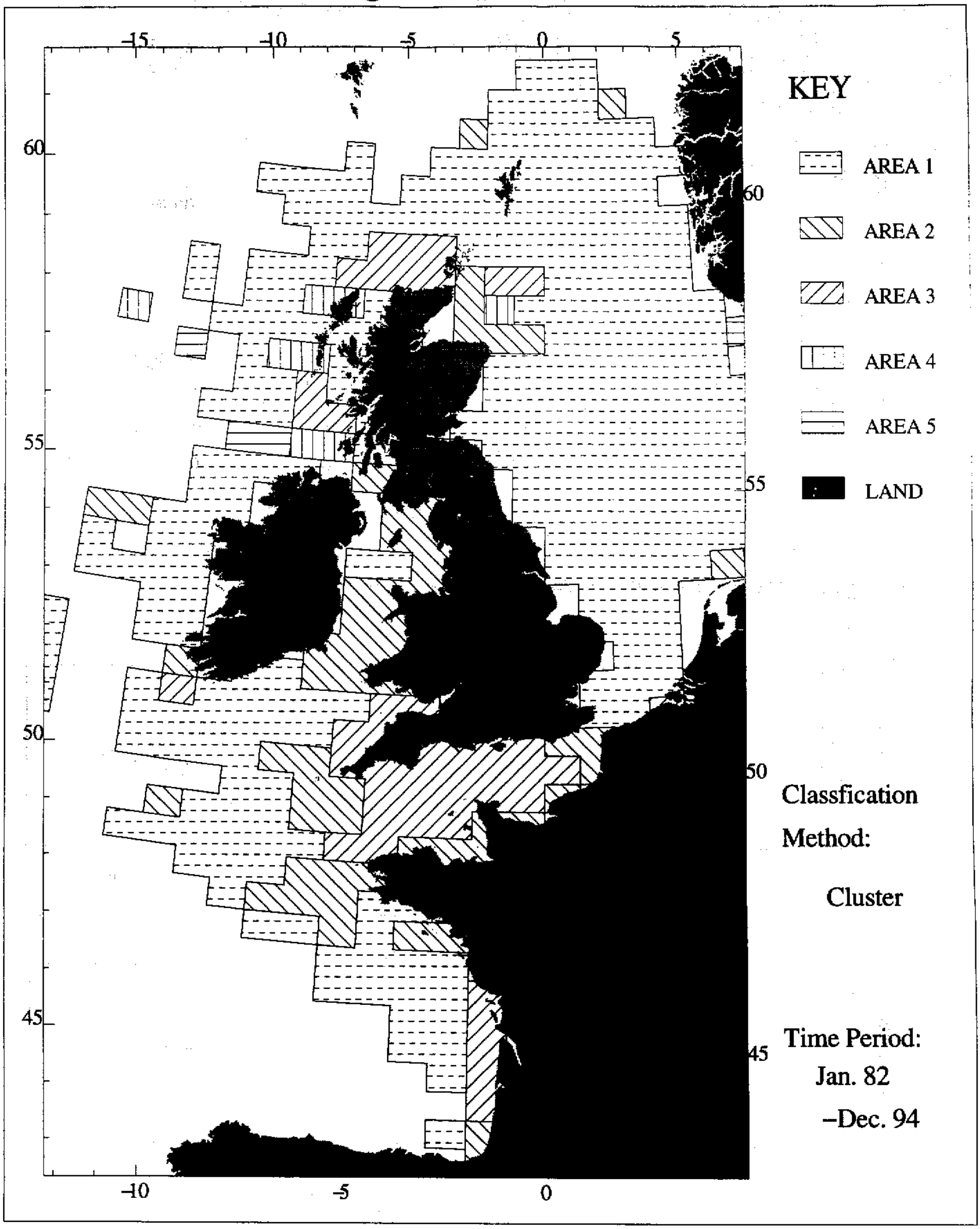


Figure 6: The classification of LPUE (*Loligo forbesi*) (156 months from January 1982 to December 1994) by use of cluster method.

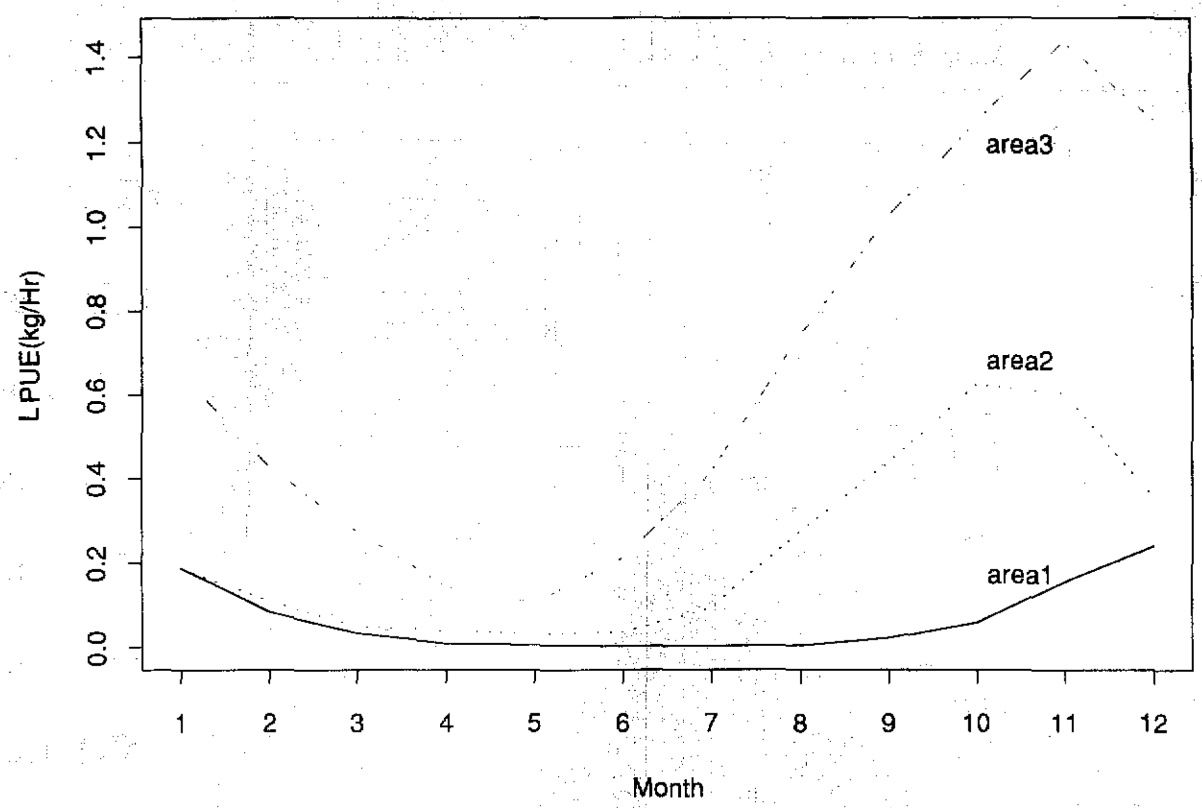
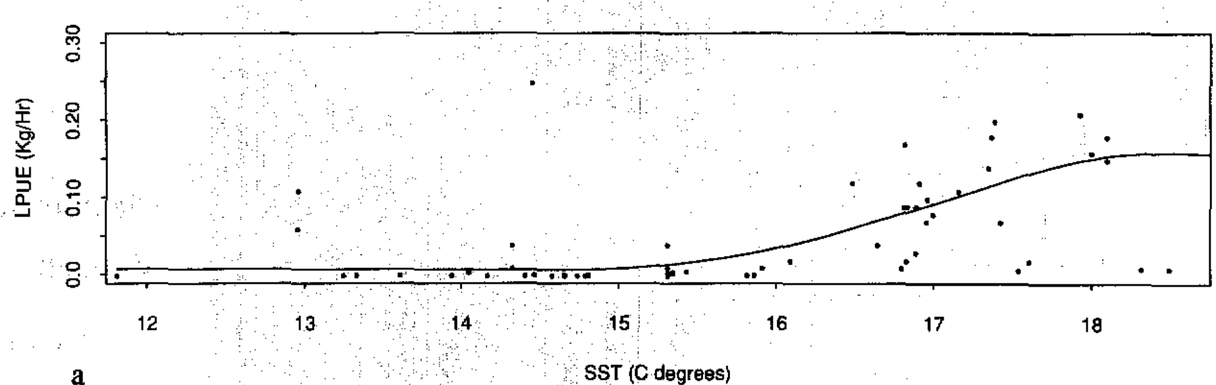


Figure 7: The seasonal pattern of LPUE of area 2, 3, and 4 (Figure 6).



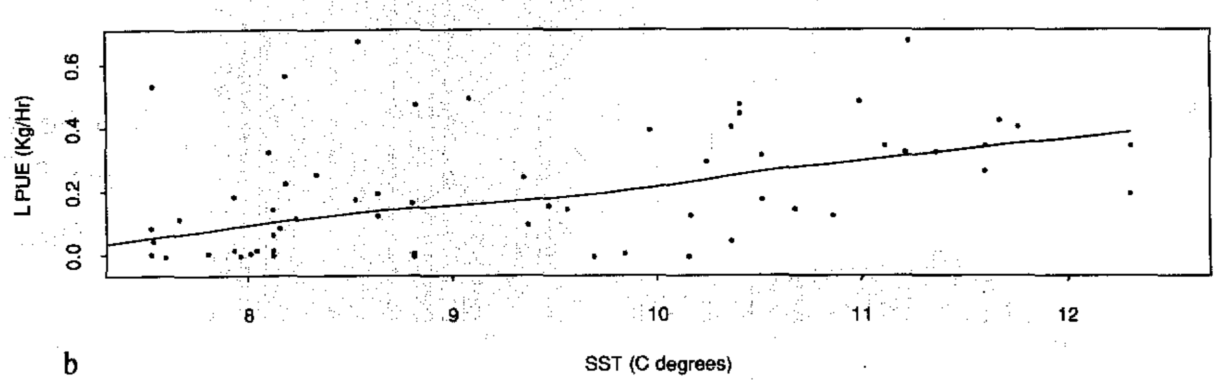


Figure 8: Squid abundance (LPUE) in relation to SST in area 2: a) LPUE in May and SST in August, b) LPUE in January and SST in January (sea text for discussion).

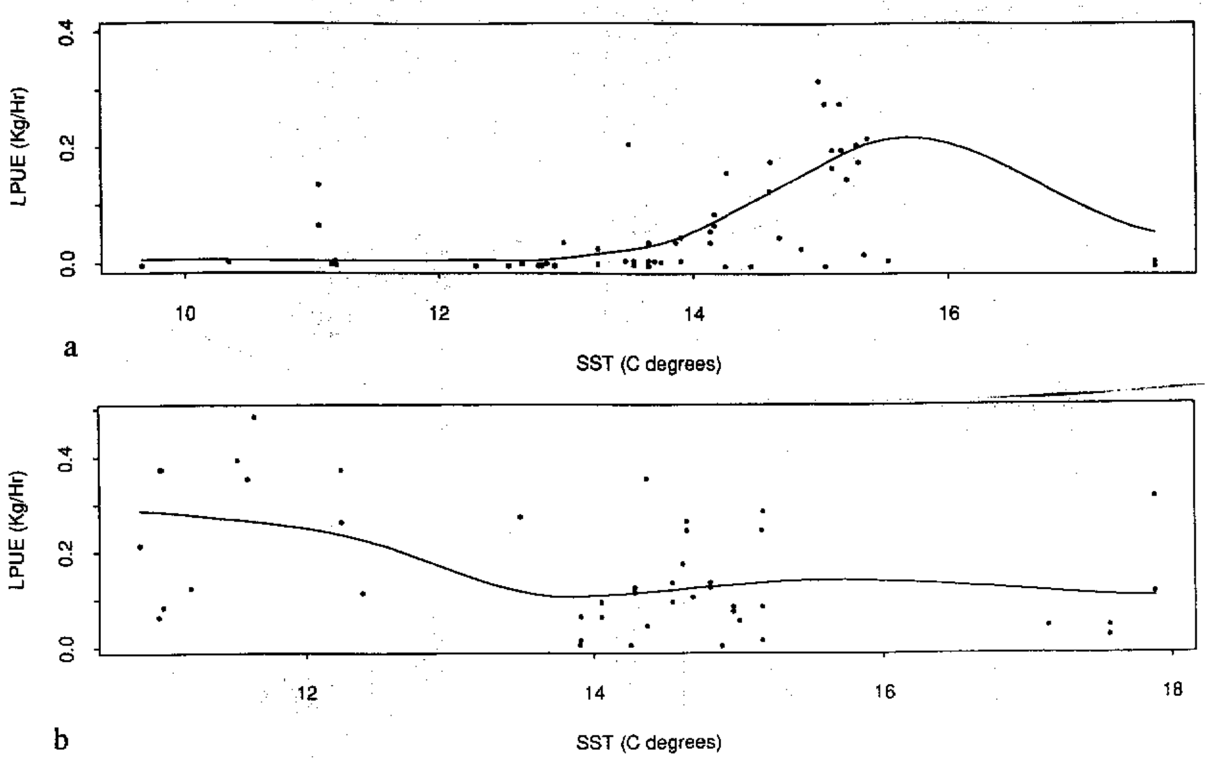


Figure 9: Squid abundance (LPUE) in relation to SST: a) LPUE in April and SST in October in area 2, b) LPUE in April and SST in august in area 3 (sea text for discussion).

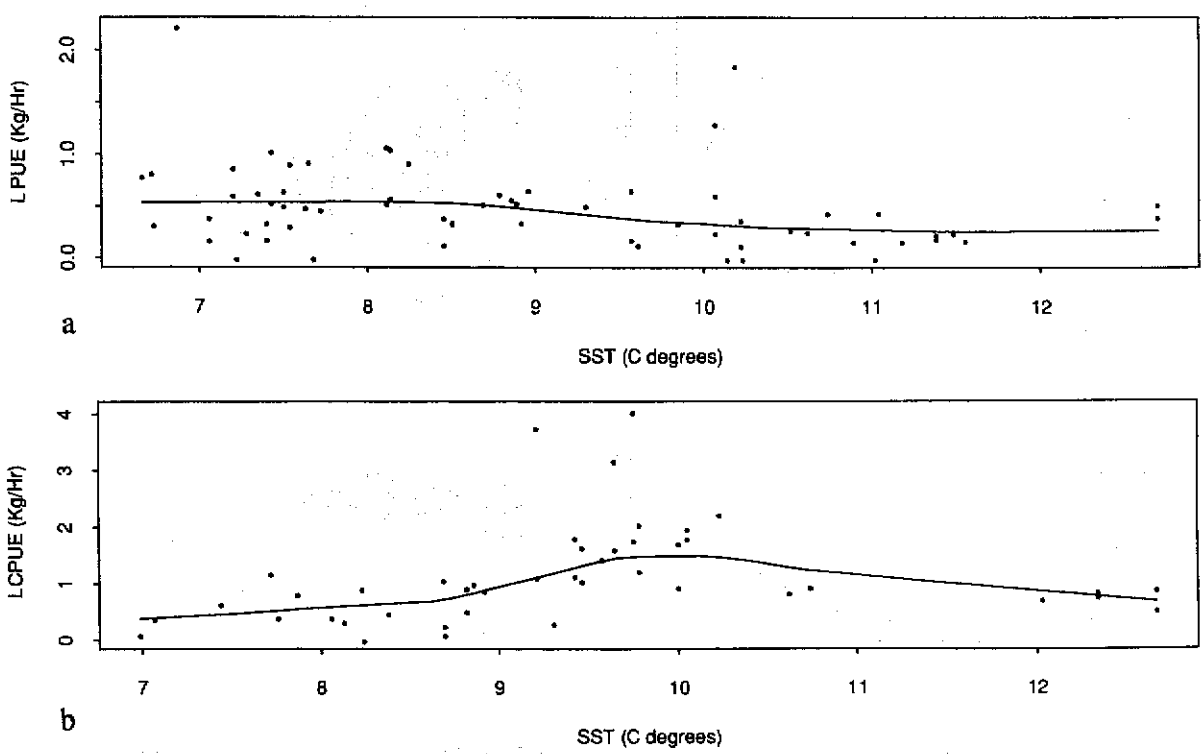


Figure 10: Squid abundance (LPUE) in relation to SST: a) LPUE in September and SST in April in area 2, b) LPUE in September and SST in April in area 3 (sea text for discussion).

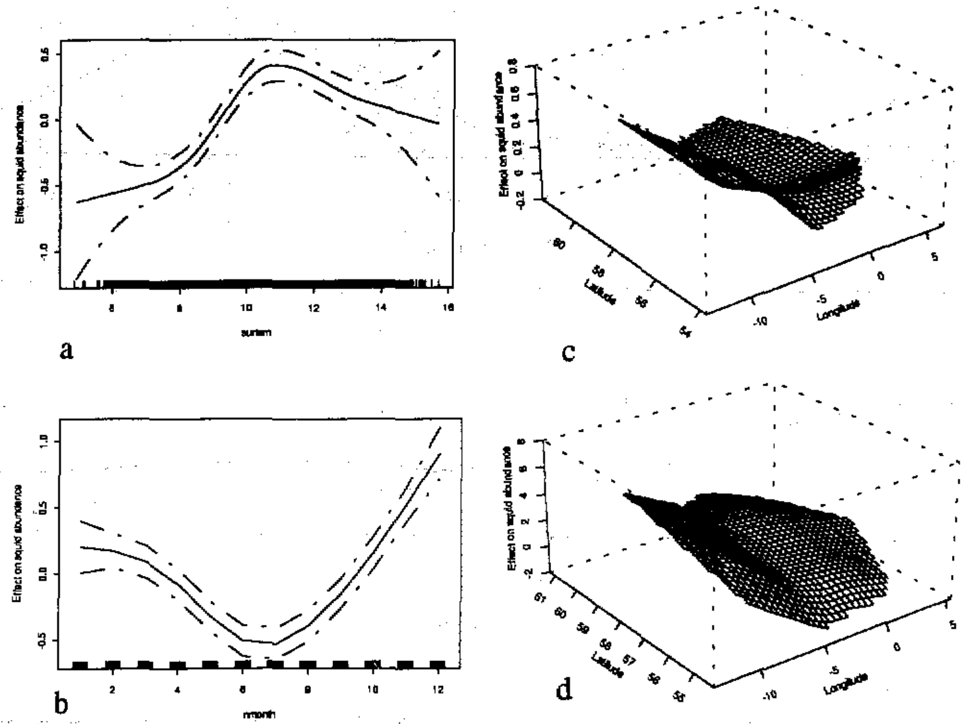


Figure 11. Results of GAM regression for 1988 squid abundance (log) given presence as a function of sea surface temperature (figure 1a) and month (figure 1b). Dashed lines represent two standard error boundaries around the covariate main effects. Perspective plots show the relationships between the geographical variables and their effect on squid abundance in June 1988 (figure 1c) and December 1988 (figure 1d).

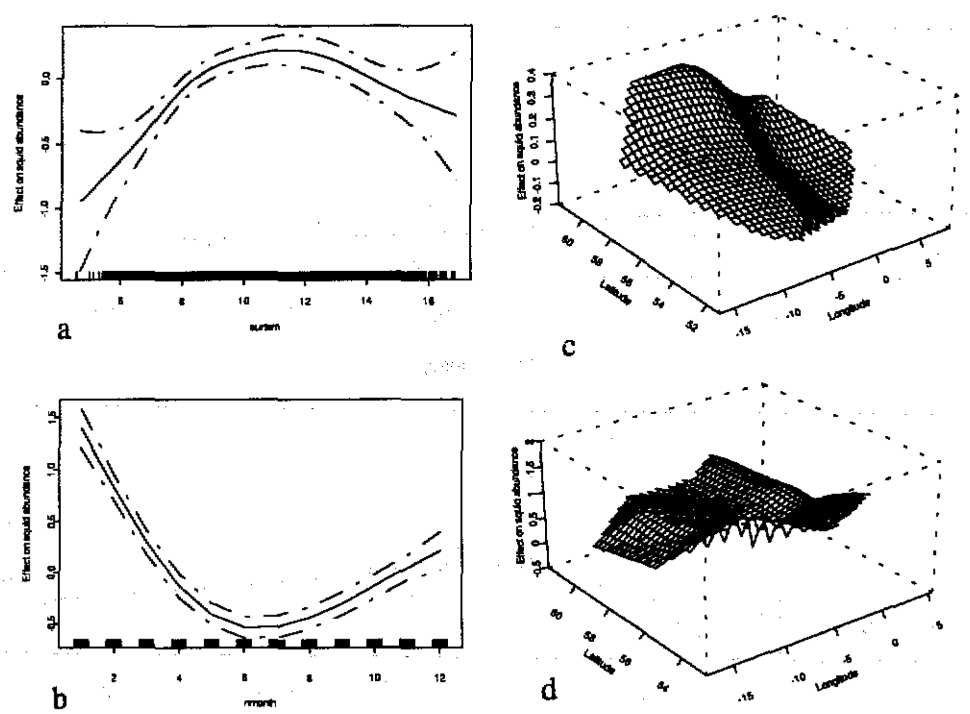


Figure 12. Result of GAM regression for 1991 squid abundance (log) given presence as a function of sea surface temperature (figure 2a) and month (figure 2b). Dashed lines represent two standard error boundaries around the covariate main effects. Perspective plots show the relationships between the geographical variables and their effect on squid abundance in June 1991 (figure 2c) and December 1991 (figure 2d).

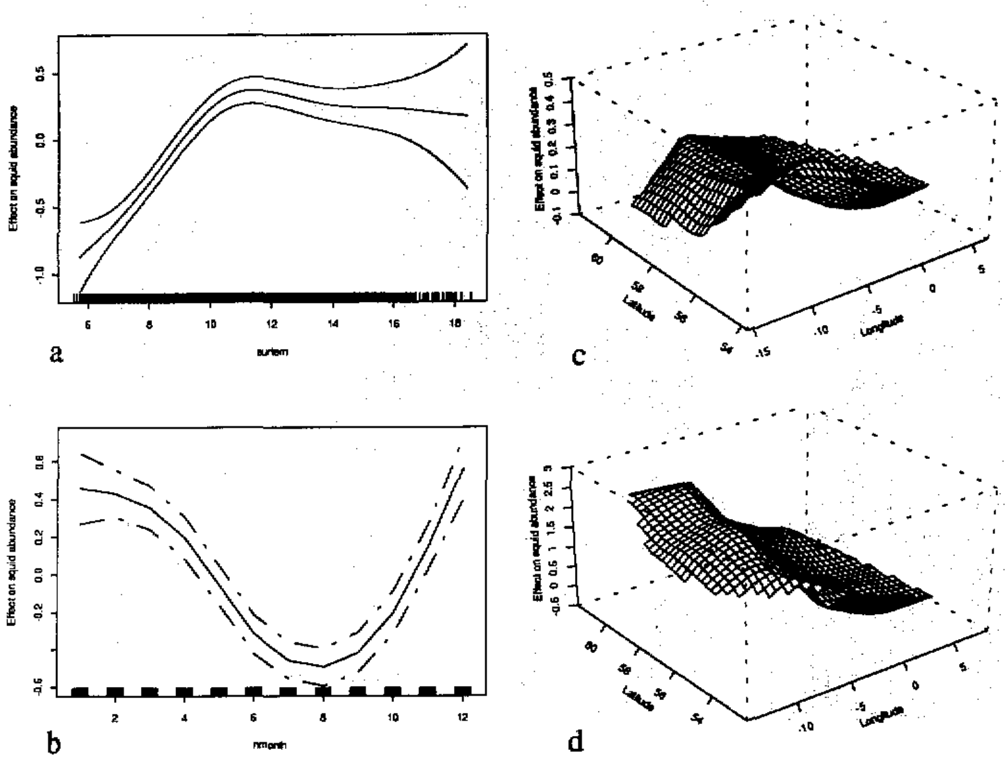


Figure 13: Result of GAM regression for 1995 squid abundance (log) given presence as a function of sea surface temperature (figure 3a) and month (figure 3b). Dashed lines represent two standard error boundaries around the covariate main effect. Perspective plots show the relationships between the geographical variables and their effect on squid abundance in June 1991 (figure 3c) and December 1991 (figure 3d).

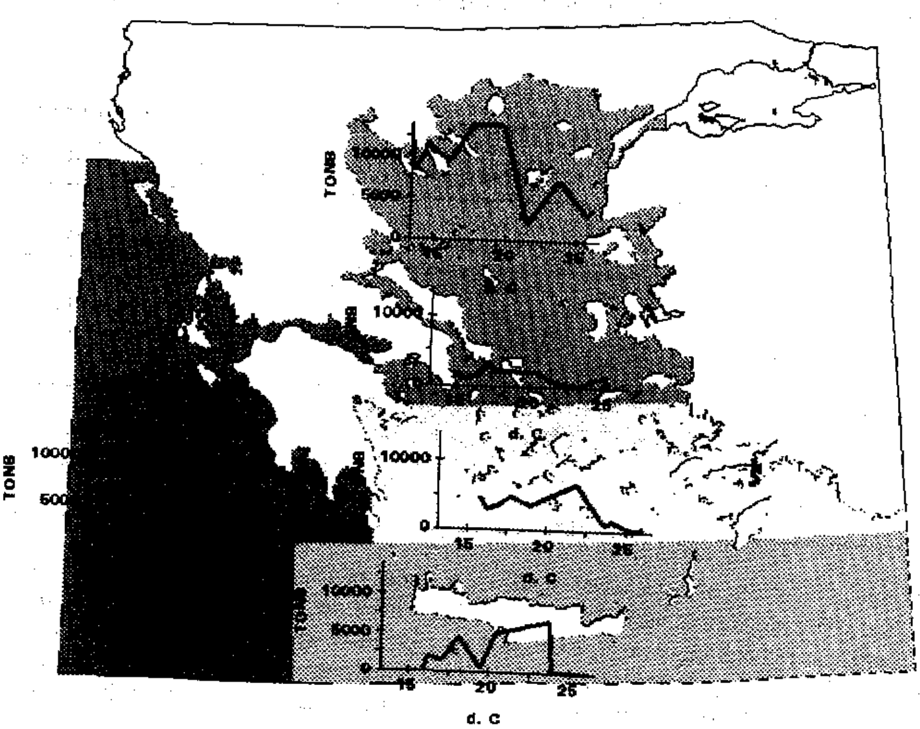


Figure 14: Distribution of total Cephalopod production (metric tons) as related to sea surface temperature (SST in degrees Celcius) for the 5 geographic areas of the Greek Seas (from top: North Aegean, Central Aegean, South Aegean, Cretan Sea, and Ionian Sea). Cephalopod species include long-fin squid (Loligo vulgaris), short-fin squid (Illex coindetii, Todarodes sagittatus), Cuttlefish (Sepia officinalis), Common octopus (Octopus vulgaris), and Musky octopus (Eledone moschata, Eledone cirrhosa).

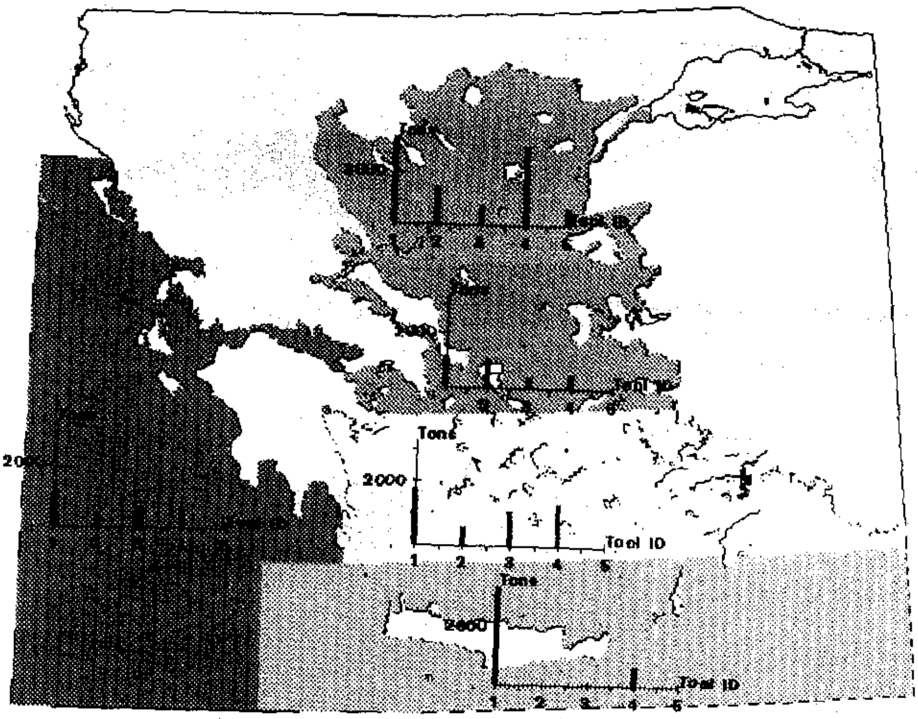


Figure14: Distribution of total Cephalopod production (metric tons) as related to different fishing gear tool (Tool ID: 1=Trawler, 2=Purse Seiner, 3=Beach Seiner, 4=Artisanal, and 5=Long-liner). Cephalopod species same as in Fig. 13.

Months with	Surface Temp	Bottom Temp	Surface Salinity	Bottom Salinity
N>20	68	60	69	63
r_s >0, P<0,01 r_s >0, P<0,05	24 28	31 38	27 33	12 19
r_s <0, P<0,01 r_s <0, P<0,05	2 4	0 0	0 0	3 6

Table I. Summary of results of correlation analysis. Number of months over the period 1989-94 in which (a) data on LPUE and oceanographic variables were available for more than 20 squares, (b) significant correlations were seen. Significant correlations are classified as (i) positive with P<0,01, (ii) positive with P<0,05, (iii) negative with P<0,01 and (iv) negative with P<0,05. For approximately 60 repeats of a two-tailed test, significant correlations (±) would be expected to occur by chance alone in no more than 1 month (for P<0.01) or 3 months (P<0.05).

	SST Jan.	SST Feb.	SST Mar.	SST Apr.	SST May	SST Jun.	SST Jul.	SST Aug.	SST Sept.	SST Oct.	SST Nov.	SST Dec.
LPUE Jan.	-0.20	-0.08	-0.07	-0.08	-0.09	-0.07	-0.15	-0.11	-0.13	-0.13	-0.01	-0.12
LPUE Feb.	0.07	0.10	0.08	0.02	0.01	0.10	0.13	0.20	0.11	0.12	0.12	0.05
LPUE Mar.	-0.13	0.01	0.01	-0.15	-0.25	-0.25	-0.22	-0.17	-0.22	-0.21	-0.12	-0.24
LPUE Apr.	-0.36	-0.19	-0.21	0.34	***-0.49***	***-0.48***	***-0.48***	***-0.50***	***-0.56***	***-0.56***	***-0.50***	***-0.49***
LPUE May	0.20	0.30	0.30	0.23	0	-0.07	-0.12	-0.22	-0.33	-0.40	-0.30	0.05
LPUE Jun.	0.17	0.29	0.27	0.16	0.12	0.02	-0.02	-0.09	-0.21	-0.29	-0.23	-0.01
LPUE Jul.	**0.60**	**0.58**	**0.57**	**0.59**	**0.51**	**0.44**	**0.49**	**0.49**	**0.48**	**0.48**	**0.54**	**0.58**
LPUE Aug.	**0.55**	**0.50**	**0.48**	**0.49**	**0.53**	**0.53**	**0.58**	**0.57**	**0.53**	**0.51**	**0.54**	**0.54**
LPUE Sept.	**0.76**	**0.71**	**0.71**	**0.74**	**0.73**	**0.67**	**0.65**	**0.58**	**0.53**	**0.52**	**0.59**	**0.74**
LPUE Oct.	**0.61**	**0.61**	**0.61**	**0.56**	**0.46**	0.38	0.38	0.30	0.24	0.21	0.30	**0.50**
LPUE Nov.	0.25	0.21	0.25	0.25	0.19	0.18	0.21	0.22	0.19	0.16	0.25	0.31
LPUE Dec.	-0.18	-0.10	-0.07	-0.23	-0.36	-0.36	-0.34	-0.32	-0.38	-0.40	-0.42	-0.25

Table 2: The correlation between monthly averaged LPUE and SST (Area3) (Jan. 1982 - Dec. 1994)

	SST Jan.	SST Feb.	SST Mar.	SST Apr.	SST May	SST Jun.	SST Jul.	SST Aug.	SST Sept.	SST Oct.	SST Nov.	SST Dec.
LPUE Jan.	**0.74**	**0.77**	**0.76**	**0.79**	**0.72**	**0.68**	**0.71**	**0.70**	**0.66**	**0.64**	**0.64**	**0.55**
LPUE Feb.	**0.72**	**0.76**	**0.76**	**0.76**	**0.73**	**0.70**	**0.74**	**0.74**	**0.72**	**0.71**	**0.70**	**0.62**
LPUE Mar.	**0.59**	**0.60**	**0.63**	**0.67**	**0.60**	**0.63**	**0.67**	**0.72**	**0.67**	**0.66**	**0.65**	**0.50**
LPUE Apr.	**0.69**	**0.69**	**0.71**	**0.72**	**0.66**	**0.70**	**0.72**	**0.77**	**0.74**	**0.76**	**0.71**	**0.56**
LPUE May	**0.71**	**0.69**	**0.71**	**0.74**	**0.71**	**0.78**	**0.79**	**0.81**	**0.74**	**0.69**	**0.72**	**0.68**
LPUE Jun.	**0.75**	**0.76**	**0.86**	**0.73**	**0.69**	**0.69**	**0.72**	**0.68**	**0.55**	**0.47**	**0.57**	**0.63**
LPUE Jul.	0.42	0.41	0.46	0.52	0.44	0.44	0.49	**0.58**	**0.54**	**0.53**	**0.56**	0.34
LPUE Aug.	-0.16	-0.22	-0.20	-0.12	-0.08	0.01	0.04	0.14	0.20	0.21	0.19	0
LPUE Sept.	***-0.45***	***-0.46***	***-0.48***	***-0.54***	***-0.51***	***-0.49***	***-0.49***	***-0.47***	***-0.44***	***-0.45***	***-0.43***	***-0.47***
LPUE Oct.	-0.38	0.42	-0.42	-0.39	-0.36	-0.37	-0.38	***-0.40***	***-0.45***	***-0.50***	***-0.45***	-0.37
LPUE Nov.	-0.09	-0.12	-0.11	-0.08	-0.06	-0.04	-0.03	0.06	0.07	-0.04	-0.06	-0.12
LPUE Dec.	0.20	0.18	0.20	0.21	0.27	0.33	0.33	0.33	0.32	0.25	0.28	0.23

Table 3: The correlation between monthly averaged LPUE and SST (Area2) (Jan. 1982 - Dec. 1994)

Formula: lpue ~ s (sst) + s (nmonth), family = gaussian.				
Year	s(surtem): Npa	Pr(F)	s(nmonth): Npa	Pr(F)
1988	14.89	1.39e-009	25.02	1.00e-01
1991	11.42	2.00e-007	69.02	0.00
1995	16.72	9.69e-011	25.01	6.70e-01

Table 4: F values and significance values (Pr(F)) for all GAM covariates. Level of significance was set to 0.05.