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Trends in abundance and geographic distribution of North Sea herring in relation to environmental factors

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ABSTRACT: Generalized Additive Models (GAMs) were used to test the hypothesis that trends in herring abundance are related to the location of ocean fronts and the temperature based variability of the northern North Sea ecosystem. Data from July of 4 years (1992 to 1995), collected during the ICES coordinated herring acoustic surveys (ICES Division IVa), were examined. It was found that geographic position and water mass characteristics influence the temporal distribution patterns of herring. The 2-stage modelling approach undertaken in the present study conveyed additional insights into the ecological behaviour of herring in the area. Temperature and depth of the thermocline, sea surface temperature, temperature difference between sea surface and seabed, and spatial location appeared to be key factors that modulate both presence and relative abundance of herring within the northern North Sea. Herring encounter was more probable in areas with cooler surface waters in the south than in the north, these areas having deeper thermoclines and temperatures at 60 m around 10°C. Results indicated that areas with higher probability of finding herring present were also located in well-mixed waters and transition zones between frontal and stratified waters. The largest herring aggregations were consistently observed in the same areas. Herring appeared to avoid the cold bottom waters of the North Sea during the summer, probably due to the relatively poor food resources there. The pronounced similarity and stability in the multiyear relationship between prespawning herring abundance, its spatial distribution and ocean environmental conditions, with and without the zero observations, support the hypothesis that the observed relationships are authentic and characteristic of the stock.

KEY WORDS: Herring (*Clupea harengus*) · Abundance · Environment · North Sea · Distribution · Generalized additive models (GAMs)

INTRODUCTION

In the marine ecosystem the dominant behavioural aspect of fish aggregation is migration to spawning grounds and spawning (Laevastu 1993). Temperature anomalies can cause changes in the timing of peak spawning and dislocation of spawning from traditional spawning grounds. Outside the spawning season, fish aggregations can be caused by feeding and migration interactions (Parrish & Saville 1965, Blaxter & Hunter 1982). For example, fish shoals slow their speed of migration in areas of abundant food such as the current boundary regions. As the speed of migration is affected by temperature and by currents, it can be expected that fish aggregations can occur at specific water type and current boundaries (fronts).

Usually the most significant horizontal temperature gradients in the sea occur in regions of divergence and convergence of currents. Currents will affect the migrations of fish by passive transport of juveniles from spawning grounds to nursery grounds, and might serve as a means of orientation of counter-current migration of adults from feeding grounds to spawning grounds. Therefore, the prediction of the positions and movements of these zones, with the meandering and eddying of water masses at their boundaries, is of great importance for the fisheries. Jakobsson (1969) stated that in most cases the densest herring concentrations in Icelandic waters during the years 1957 to 1966 were located at, or just outside, the continental shelf in the

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boundary areas of warm and cold water masses. Furthermore, the concentrations usually extended along the current boundaries but had a less extensive distribution pattern in other directions.

In the northern North Sea the herring-environment relationship has been proposed since the early days of fisheries science (Hardy 1936 and references therein). The study area is a hydrographically dynamic area. In July the main feature is the Slope Current, which is responsible for the input of nutrient rich water west of the Shetland and Orkney Islands, UK. Some of this water enters the North Sea via the East Shetland Atlantic Inflow (ESAI, flowing north and then east of the Shetland Isles) and the Fair Isle Current (flowing between Shetland and Orkney; Fig. 1). Sea surface temperature (SST) values around 12°C are characteristic of water of Atlantic origin inundating into the northern North Sea (Turrell 1992). The ESAI is characterized by SST around 12°C inshore and around 13°C offshore from the islands. The temperature difference between sea surface and seabed for the areas adjacent to the Slope Current and ESAI is usually of the order of 2 to 4°C. The central northern North Sea is characterized by SST around 13°C (Turrell & Slesser 1992).

A previously suggested hypothesis, that of the relationship of herring distribution to the temperature based variability of the ecosystem and the presence of boundary zones (Maravelias & Reid 1995, 1997), was further examined here. In the present study 4 years' data, collected from acoustic surveys carried out in July 1992 to 1995 in the northern North Sea (Orkney/Shetland area, ICES Division IVa; Fig. 1), were analysed (area boundaries 58° 30' to 62° N and 4° W to 2° E). The analysis of 4 years of consecutive acoustic surveys allowed the examination of whether the geographic distribution of herring during the summer in the North Sea is similar between years and whether the spatial abundance of herring is affected by environmental factors in a similar manner across the study years. Herring (*Clupea harengus* L.) come into the area from the north as part of the annual cycle of migration and are believed to head subsequently towards the spawning grounds around the Orkney and Shetland Islands and Scotland (Corten & van de Kamp 1992). The goal of the present work was to model the dependence of herring abundance on the abiotic factors examined and establish quantitative relationships between them. The objective was to learn more about the variables that drive the process of prespawning herring distribution and determine spatial abundance.

MATERIALS AND METHODS

Data collection. The surveys were carried out on prespawning concentrations of autumn spawning herring during July 1992 to 1995 using the Simrad EK500 38 kHz sounder and echo-integrator on board the Fisheries Research Vessel 'Scotia' (details of equipment are reported in Simmonds et al. 1996). Further data analysis was carried out using Simrad BI500 and Marine Lab Analysis systems. The survey track was designed to cover the area generally at a single level of sampling intensity based on the limits of herring densities found in the previous years, with the majority of transect spacings set at 15 nautical miles (n miles). The ends of the tracks were positioned at half the actual track spac-

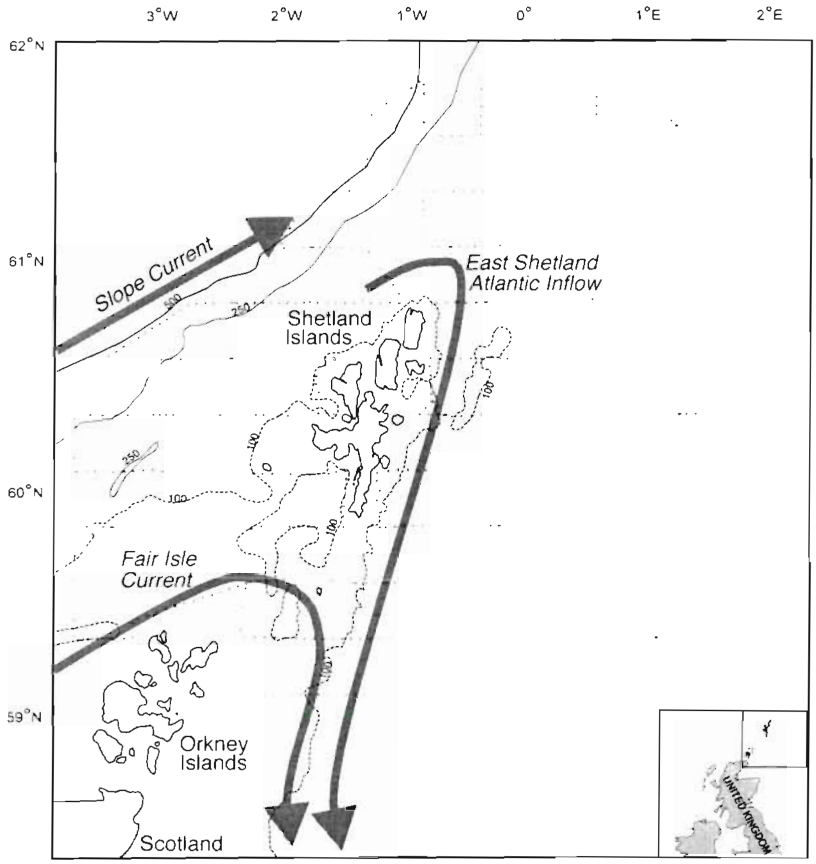

Fig. 1 Bottom topography (m) of the study area, northern North Sea (ICES Division IVa). Arrows indicate main currents and water movements in the area. (+++) Survey track of FRV 'Scotia' during the 1992 survey

ing from the area boundary, giving equal track length in any rectangle within the area. Data from the echo integrator were summed over quarter hour periods (2.5 n miles at 10 knots). Trawl hauls were carried out during the survey on the denser echo traces. The trawl hauls were used to partition school echo integrals between species, based on trawl composition. The bulk of the hauls were predominantly herring. A detailed description of the proportion of herring in the echo traces can be found in Simmonds et al. (1996). Each haul was sampled for length, age, maturity and weight of individual herring. The herring density data were available on a fine scale along the survey track (every 2.5 n miles) in the form of herring echo abundance index (EAI). This abundance index was calculated from the fraction of the echo integral identified, by trawl, as herring and is linearly related to herring biomass (Foote 1983). The herring migration speeds have been estimated to be approximately 1 n mile d^{-1} (Simmonds 1995) while the time between adjacent transects is 24 h; thus migration while present is a minor problem. Consequently these surveys are regarded as good indicators of the spatial structure of the population (Maravelias & Reid 1997). SST values were obtained from a shipboard thermosalinograph (Ocean Data model TSG103) connected to the vessel's non-toxic seawater supply, which recorded values at 3 m depth. Conductivity, temperature and depth (CTD) data were collected during the 1994 and 1995 surveys (a total of 141 stations).

Data analysis. Vertical profiles of temperature and salinity were available only for 1994 and 1995, therefore the analysis inevitably fell into 2 parts; firstly, 1992 and 1993 included latitude, longitude, SST and secondly, 1994 and 1995 with the addition of CTD (both years) and Expendable Bathythermographs, i.e. XBT (1995 only) vertical profiles. From these vertical profiles for 1994 and 1995 the following additional parameters were extracted: the temperature at 60 m depth, the bottom temperature and the depth of the thermocline. Thermocline depth was taken as the depth at which temperature had dropped by 90% of the difference between surface and 60 m temperatures after observing that on most casts the thermocline occurred at depths less than 60 m. This definition of the thermocline is consistent with the hydrography of the study area (W. Turrell, Oceanography Section, FRS Marine Laboratory, pers. comm.) and has been used in similar studies (Swartzman et al. 1995, Maravelias & Reid 1997). The local regression model *loess* (Cleveland & Devlin 1988) was used to model temperature at 60 m depth, thermocline depth and the bottom temperature as a function of depth, latitude and longitude and then *loess* was used in a predictive mode to interpolate the values at the herring EAI locations. Scatter plots of the relationship of herring abundance to all the studied variables were produced in order to visualize and suggest possible relationships between the variables. These relationships were further examined and tested using generalized additive models (GAMs) (Hastie & Tibshirani 1990).

Generalized additive models. GAMs were used to model trends in herring abundance distribution (1992 to 1995) as functions of geographic position and ocean environmental variables with the main aim being to draw inferences for the mechanisms that give rise to the distribution of herring. The theory of GAMs is described in great detail in Hastie & Tibshirani (1990) and in Swartzman et al. (1992) for an application in fisheries. In GAMs the dependent variable, here herring abundance, is modelled as the additive sum of unspecified non-parametric smooth functions of hypothesized covariates and their interactions. Backward stepwise elimination was used to select a set of significant covariates by minimizing the Akaike's Information Criterion ($AIC = deviance + 2 \cdot df \cdot \varphi$, where df is the degrees of freedom in the fit and φ is an estimate of the dispersion parameter). The model that resulted in the biggest decrease in AIC was selected as the best-fitting model. Examination of the deviances and the differences in deviances that arise was also performed. To evaluate these differences and compare the models, approximate *F*-tests based on the approximate degrees of freedom and the corresponding percentage point of the *F*-distribution were computed, as suggested by Hastie & Tibshirani (1990). The S-PLUS software employed for the GAM analysis computes only asymptotic approximations of pointwise standard-error bands under the serious assumptions of Gaussian errors and negligible bias. Evidently, these are inappropriate for construction of pointwise confidence intervals (Hastie & Tibshirani 1990). As a result, in the present paper estimates of variability in GAMs were obtained using bootstrap methodology (1000 samples). The significance of these trends was determined by means of permutation tests (700 permutations; Venables & Ripley 1994). For a detailed description of the bootstrap methodology and the permutation tests as these were applied in the present work see Swartzman et al. (1992) and Borchers et al. (1997).

One obvious characteristic of acoustic survey data is the large number of zero observations. Data with such a high proportion of zeros are usually difficult to model in 1 step. Here I implemented a 2-stage model: firstly model the probability of presence of herring, and secondly the number of herring (abundance as EAI) given that some were observed. A GAM with logit link, binomial error structure was found to be adequate for the first stage of modelling, whereas for the second stage a log link function with Gaussian error distribution was chosen. In GAMs the least squares estimate of the multiple linear regression is replaced by a local smoother In the present study the cubic spline smoother, s (Hamming 1973), was used. The degree of smoothing performed by the smoother, $s_k()$, is determined by the degrees of freedom associated with the smooth; the fewer the df, the less flexible the function. The degree of smoothness was determined on the basis of the observed datasets. To facilitate the problem of selecting the amount of smoothing for a given term, its df were fixed according to the proposal of Hastie & Tibshirani (1990); for an application see also Borchers et al. (1997). That is, for the covariates already selected, backward stepwise selection was performed between the fit having a covariate with smoothing spline with df = 4 and the same but with df = 1 (i.e. linear fit; Hastie & Tibshirani 1990, Borchers et al. 1997). Analysis of variance (ANOVA) was used to compare models by analysing changes in deviances relative to the changes in degrees of freedom.

All available variables and their first order interactions were initially included in the model. Latitude was used as a measure of spatial location (longitude was found to be non-significant) and the differences between surface and bottom temperature values were

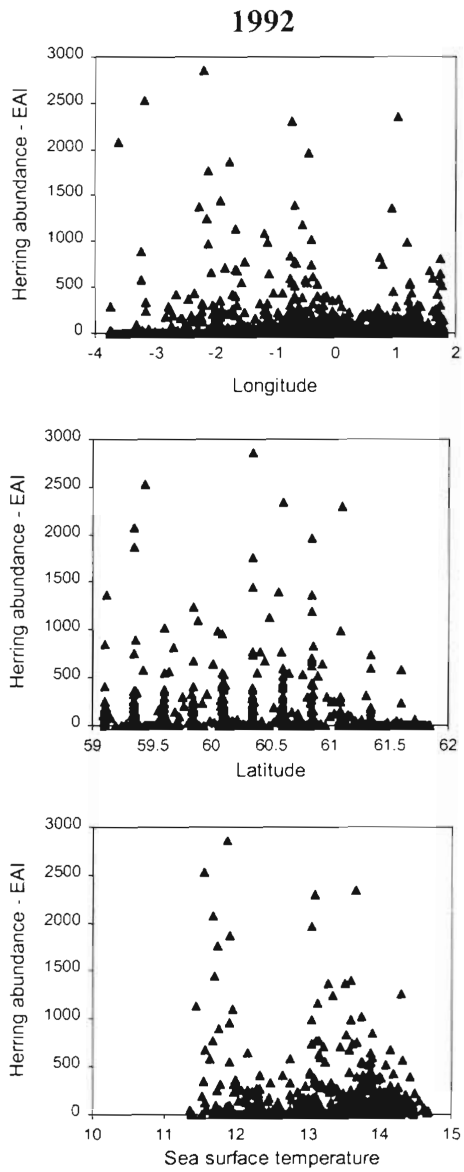

Fig. 2. Scatterplots between herring abundance (EAI values) and longitude, latitude and sea surface temperature (°C) for the 1992 survey. Longitude: negative values correspond to west, positive to east

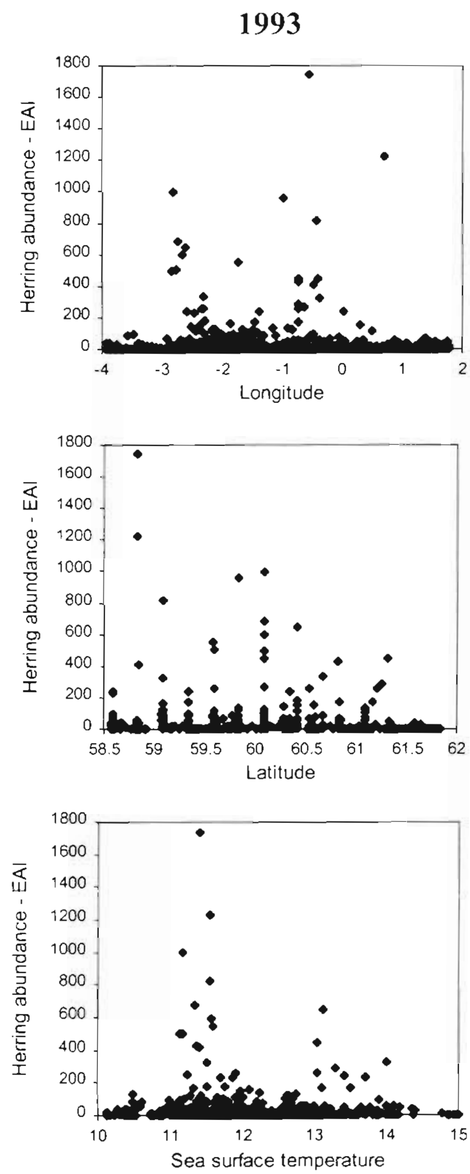

Fig. 3. Scatterplots between herring abundance (EAI values) and longitude, latitude and sea surface temperature (°C) for the 1993 survey. Longitude as in Fig. 2

used as indicators of mixing/stratification and presence of currents and frontal areas (W. Turrell pers. comm.).

RESULTS

A schematic of the study area and the main currents in the northern North Sea is given in Fig. 1. The scatter plots for each studied year (1992 to 1995) are presented in Figs. 2 to 5 respectively. These suggested the following relationships for each factor examined:

(1) No clear relationship could be demonstrated between longitude and herring abundance. High fish values were found at almost every longitude value.

(2) A more obvious pattern with regard to herring latitude preferenda was evident. Latitude values from 60° to 61° N and around 59.5° N appeared to be associated with high herring abundances.

(3) The larger herring aggregations were consistently found in SST ranges between 11 and 12°C (around 12°C for 1995) and between 13 and 14°C. This is a noteworthy pattern of association, in the sense that it is repeatedly observed throughout the studied period (i.e. 4 years).

(4) A deep thermocline (>30 m) was associated with high herring biomass, although there was some evidence for herring being present at shallower thermoclines (Figs. 4 & 5).

(5) Temperatures at 60 m depth between 9 and 11°C were associated with high herring abundance (Figs. 4 & 5).

(6) Areas dominated by fronts and currents (i.e. surface – bottom temperature difference close to zero) were characterized by low herring abundance; transition zones (i.e. intermediate surface – bottom temperature difference) were associated with the highest herring abundances (Figs. 4 & 5).

The results of the GAM models are shown as plots of the best-fitting smooths for the effect of the covariates

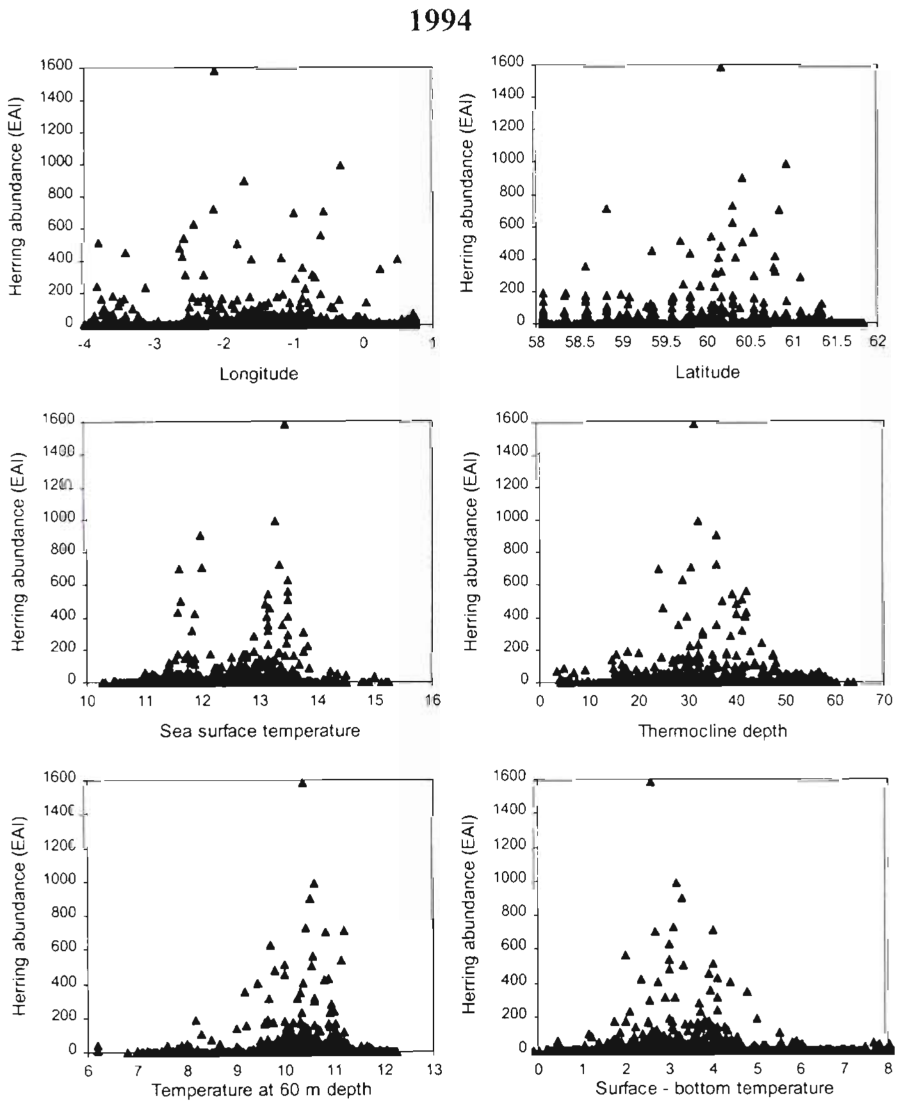

Fig. 4. Scatterplots between herring abundance (EAI values) and longitude, latitude, sea surface temperature (°C), thermocline depth (m), temperature at 60 m (°C) and the temperature difference between surface and bottom water (°C) for the 1994 survey. Longitude as in Fig. 2

on the parameter of interest, i.e. herring abundance. The 95% confidence intervals are also plotted around the best fitting smooths for the main effects. 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. Interaction effects are shown as perspective plots without error bounds. The y-axis reflects the relative importance of each covariate of the model; the interaction effects are presented on the z-axis. These results are presented in Figs. 6 to 9 for the first stage of modelling, i.e. presence/absence of herring (modelling the probability of finding herring present) and in Figs. 10 to 13 for the second stage of modelling, i.e. modelling herring density after conditioning on the presence of herring.

It needs to be emphasized that the effect of each variable shown in the above figures is the conditional effect, that is, the effect that this variable has, given that the other variables are included in the model. In Table 1 the significance values (p-levels) of GAM covariates for all years are given.

First stage GAM model

In the first stage, the presence/absence of prespawning herring was modelled (i.e. the probability of finding fish present). Latitude and SST in all 4 years and surface – bottom temperature and thermocline depth (either as a main effect or interaction) in 1994 and 1995 were found to be highly significant covariates (Table 1a). The temperature at 60 m-thermocline depth interaction in 1994 was also significant.

The area where the probability of finding prespawning herring present was high was progressively confined to more southern limits from 1992 to 1995. More

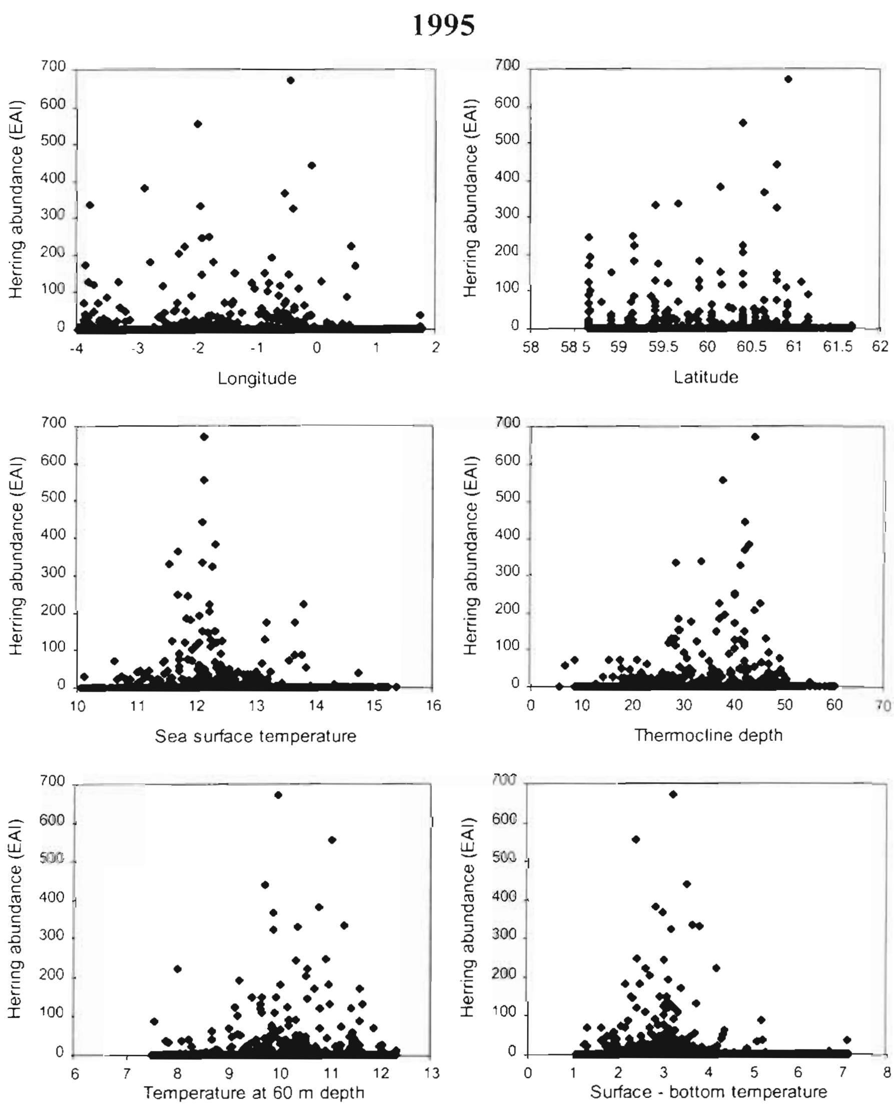

Fig. 5. Scatterplots between herring abundance (EAI values) and longitude, latitude, sea surface temperature (°C), thermocline depth (m), temperature at 60 m (°C) and the temperature difference between surface and bottom water (°C) for the 1995 survey. Longitude as in Fig. 2

Table 1. Results of permutation tests showing the significance values (p-levels) for all GAM covariates and their interactions. (a) First stage and (b) second stage GAM models. Level of significance was set at 0.05. ns: non-significant. na: covariates not available for 1992 and 1993

Covariate	1992	1993	1994	1995
(a) Presence/absence				
Latitude	0.001	0.001	0.001	0.001
Sea surface temperature (SST)	0.001	0.001	0.009	0.03
Latitude-SST interaction	ns	ns	ns	ns
Thermocline depth	na	na	ns	0.001
Surface – bottom temperature	na	na	0.001	0.001
Temperature at 60 m - thermocline depth interaction	na	na	0.001	ns
(b) Herring density given presence				
Latitude	0.001	0.001	0.001	0.001
Sea surface temperature (SST)	0.001	0.016	0.02	0.001
Latitude-SST interaction	0.002	0.008	ns	ns
Thermocline depth	na	na	0.001	0.001
Surface – bottom temperature	na	na	0.01	0.04
Temperature at 60 m - thermocline depth interaction	na	na	0.001	0.001

precisely: in 1992 the area with the higher probabilities of finding herring present extended from 59.5° to 61.2° N (Fig. 6). In 1993 the northern limit of this area was south of 61° N (Fig. 7). In 1994 the area with the highest probability of finding herring present was south of 60° N with an increasing probability of finding high concentrations of prespawning herring in the southern limits of the survey area (latitudes lower than 59° N; Fig. 8). In 1995 this latter trend continued (Fig 9), alongside a distinct preference for the area between 60.5° and 61° N.

The main effect of SST was revealed by the shapes of the smooths in Figs. 6 to 9. A distinct preference for warmer surface waters was displayed for the years 1992 and 1993. Surface waters with temperatures greater than 13.2°C in 1992 and 12.3°C in 1993 exhibited a significant main effect on fish presence. For 1992 the high probability encountered in lower SST values (Fig. 6) was due to few observations (see rug) and was therefore treated with caution. For the following 2 years the waters with the higher probability of finding herring present continued to be characterized by grad-

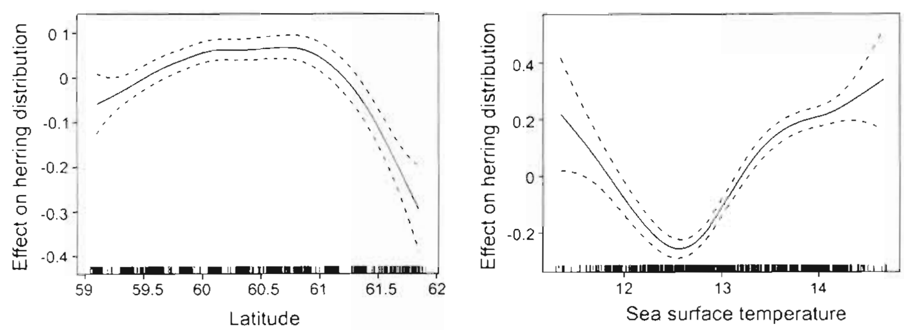

Fig. 6. GAM regression for 1992 herring presence/absence as a function of latitude and sea surface temperature (°C). Dashed lines: 95% confidence limits around the covariate main effects obtained from bootstrap resampling of the original data

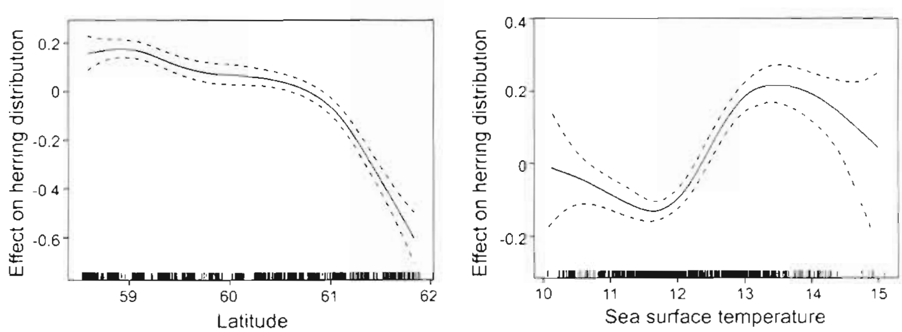

Fig. 7. GAM regression for 1993 herring presence/absence as a function of latitude and sea surface temperature (°C). Dashed lines as in Fig. 6

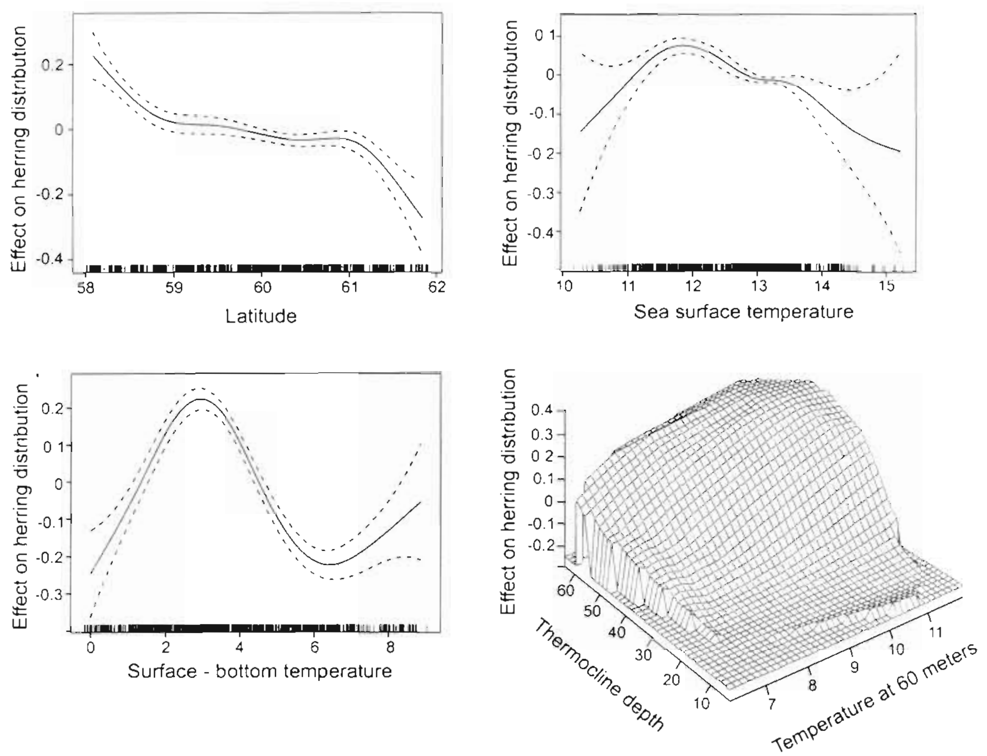

Fig. 8. GAM regression for 1994 herring presence/absence as a function of latitude, sea surface temperature (°C), temperature difference between surface and bottom waters (°C) and the interaction of temperature at 60 m depth (°C) with thermocline depth (m). Dashed lines as in Fig. 6

ually cooler surface temperatures. In 1994 these were waters with SST between 11 and 12.8°C and in 1995 waters with SST between 10.8 and 12.5°C. However, for both 1994 and 1995, the effect of the SST on the presence of herring was similar, as evidenced from the shapes of the smooths in Figs. 8 & 9.

The probability of finding herring present was higher in transition zones between frontal and stratified waters (intermediate surface – bottom temperature values) and lower in stratified waters (larger surface – bottom temperature values). This was confirmed in both 1994 and 1995 (Figs. 8 & 9).

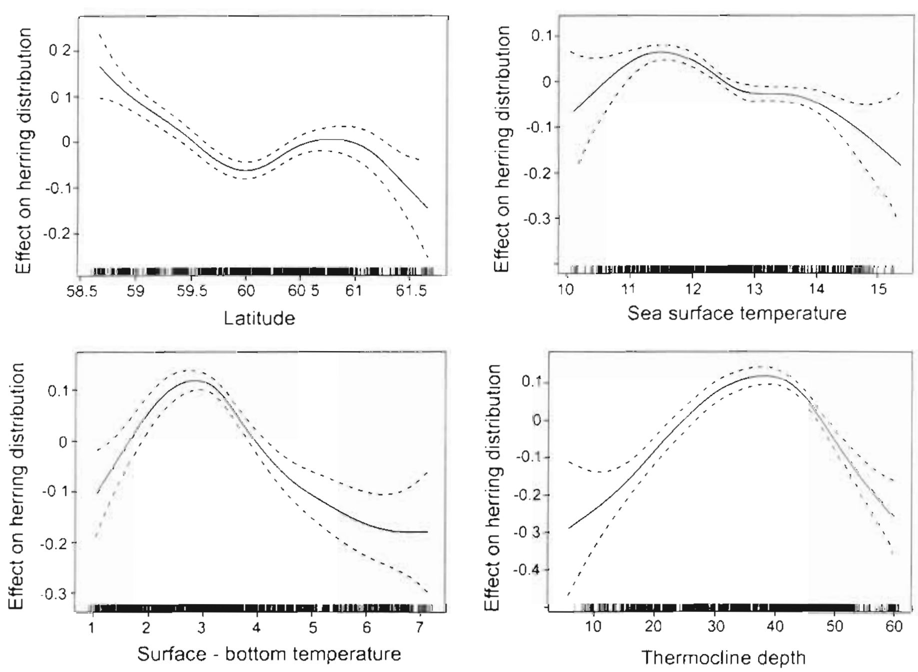

Fig. 9. GAM regression for 1995 herring presence/absence as a function of latitude, sea surface temperature (°C), temperature difference between surface and bottom waters (°C) and thermocline depth (m). Dashed lines as in Fig. 6

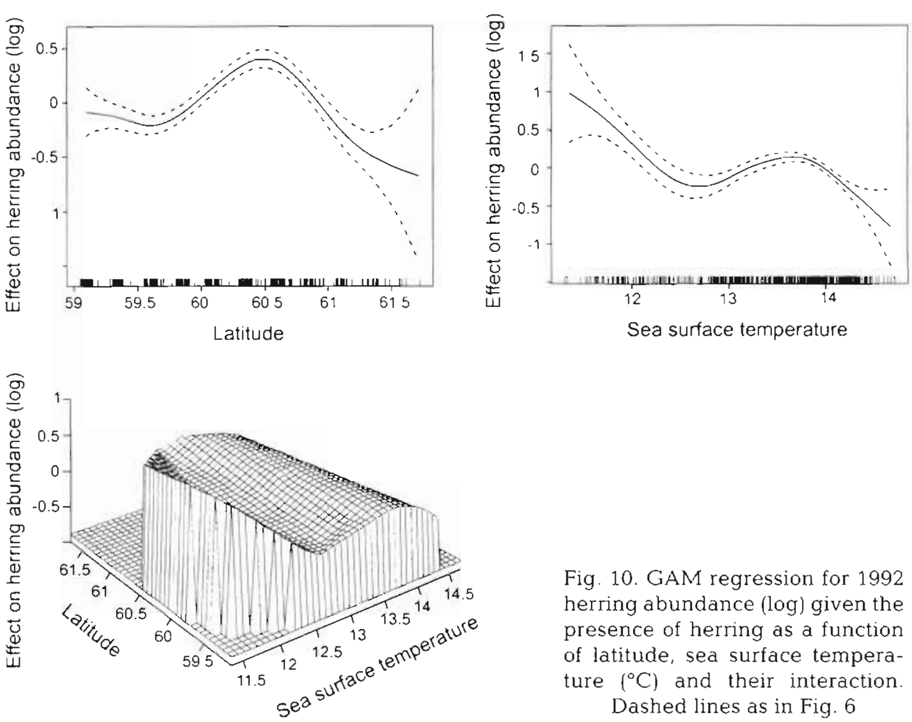

Fig. 10. GAM regression for 1992 herring abundance (log) given the presence of herring as a function of latitude, sea surface temperature (°C) and their interaction. Dashed lines as in Fig. 6

The depth of the thermocline was also found to be an important factor controlling the presence of fish. In 1994, thermocline depth affected herring presence through its interaction with the temperature at 60 m depth. There was a higher probability of herring being present in areas with deeper thermoclines (up to 55 m) and warmer temperatures at 60 m (9 to 11°C) (Fig. 8). Apparently the probability was the highest when the thermocline was forming in 40 m depth and the temperature at 60 m was around 10°C. In 1995 thermocline depth exhibited a main effect on fish presence. Prespawning herring were more likely to be found in areas with thermoclines formed between 25 and 45 m. The highest probability of finding herring was observed in areas having a thermocline depth around 40 m (Fig. 9), as in 1994.

Second stage GAM model

In the second stage, the herring density was modelled given the presence of herring. The significance values are given in Table 1b. The latitude and SST in all 4 years, their interaction in 1992 and 1993, the thermocline depth as a main effect and as interaction with temperature at 60 m in 1994 and 1995 and finally the temperature difference between surface and bottom waters in 1994 and 1995 were all found to modulate the distributional abundance of herring in the studied area. The latitude, the thermocline depth and the temperature at 60 m - thermocline depth interaction were highly significant.

An obvious feature of the GAM plots of this stage is the change in the shapes of the smooths (Figs. 10 to 13) compared with the ones already examined (Figs. 6 to 9). This is due to the fact that it was herring density that was modelled here conditioned on the presence of herring. Therefore, the zero observations were not considered in the models and thus did not mask any herring-covariate relationship.

Herring abundance was highest at latitudes around 60° to 60.5° N. Average herring abundance was high for latitudes between 59.5° and 61° N. Average herring abundance was decreasing each year, which is confirmed by a closer examination of the *y*-axes scale of the effect plots (Figs. 10 to 13). This became more apparent in 1995 when the average herring density was found to be low over most of the survey area (Fig. 13). In all 4 years northern latitudes (>61° N) were associated with a lack of fish.

SST ranges between 11 and 12°C and between 13 and 14°C were related to high average herring abundances. In 1992 and 1993, southern (<60.5° N) cooler surface waters (SST < 12°C) were associated with the highest herring abundances (Figs. 10 & 11).

Herring abundances were, on average, greatest for thermocline depths around 40 m and high for thermocline depths between 25 and 45 m (Figs. 12 & 13). Areas with a surface – bottom temperature value around 3°C were associated with high herring densities. When the

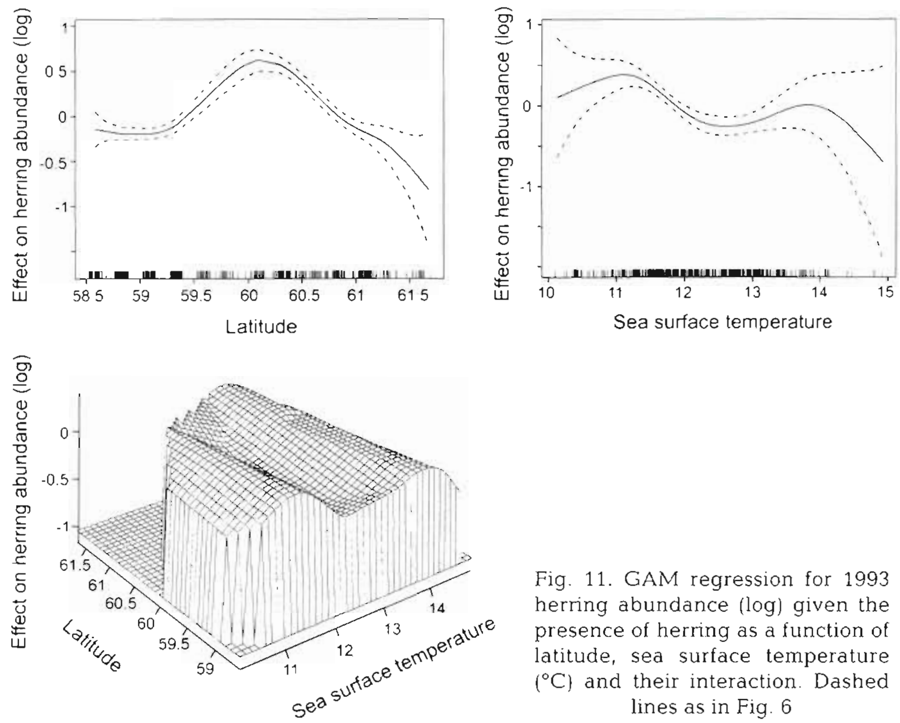

Fig. 11. GAM regression for 1993 herring abundance (log) given the presence of herring as a function of latitude, sea surface temperature (°C) and their interaction. Dashed lines as in Fig. 6

temperature at 60 m was between 9 and 11°C, there was an increase in average herring abundance with increasing thermocline depth up to 45–50 m. The effect of the thermocline depth on herring abundance was greater at warmer temperatures at 60 m (around 10°C).

DISCUSSION

A large number of zero value observations is a rather typical phenomenon in fisheries surveys. The analysis of such data is somewhat problematic because zero value observations could mask the underlying spatial dependence of species on environmental factors. The 2-stage modelling approach undertaken here is an attempt to efficiently detect the spatial trends in the distribution patterns and quantitatively identify the relationships between herring and environmental factors. This analysis is also qualitatively different from the ones previously applied (Swartzman et al. 1992, 1995, Maravelias & Reid 1997), since it modelled presence/absence separately from the abundance where fish were present. The significant variables for the first stage GAM (presence/absence) could be interpreted as the ones that might drive the process of prespawning distribution (i.e. of there being any herring present), whereas the significant variables from the second stage GAM can be interpreted as the ones that might determine whether there are few or many herring there, given that some herring are there (Borchers et al. 1997). Evidently, this analysis provided additional information on the ecological behaviour of the species.

The present results supported the hypothesis that the temperature profile of the water column and the geographic location seemed to be significant factors that might modulate both presence and relative abundance of herring within the northern North Sea ecosystem. This study also demonstrated that all the variables studied appeared to have an impact on herring distribution either as a main or as an interactive effect. There is a strong consistency in the pattern and significance of the observed relationships across all 4 years of the study. However, it is more than likely that other factors not examined here (such as water depth and seabed substrate) may also be important.

The northern limit of herring distribution was usually found to be at 61° N, corresponding to the latitude of the northern tip of the Shetland Islands. Herring showed a consistent preference for latitudes around 60.5° N, although a southward progressive shift of the population was also observed. In 1992, herring encounter was more probable in latitudes between 59.5° and 61.2° N with SST lower than 12 and higher than 13°C (first stage GAM), but the larger herring aggregations were limited to between 59.9° and 60.9° N (second stage GAM) and SST mainly lower than 12°C. In 1993 southern latitudes (lower than 60.8° N) and SST warmer than 12.5°C were found to affect prespawning distribution (first stage GAM). However, the largest herring aggregations were once more lim-

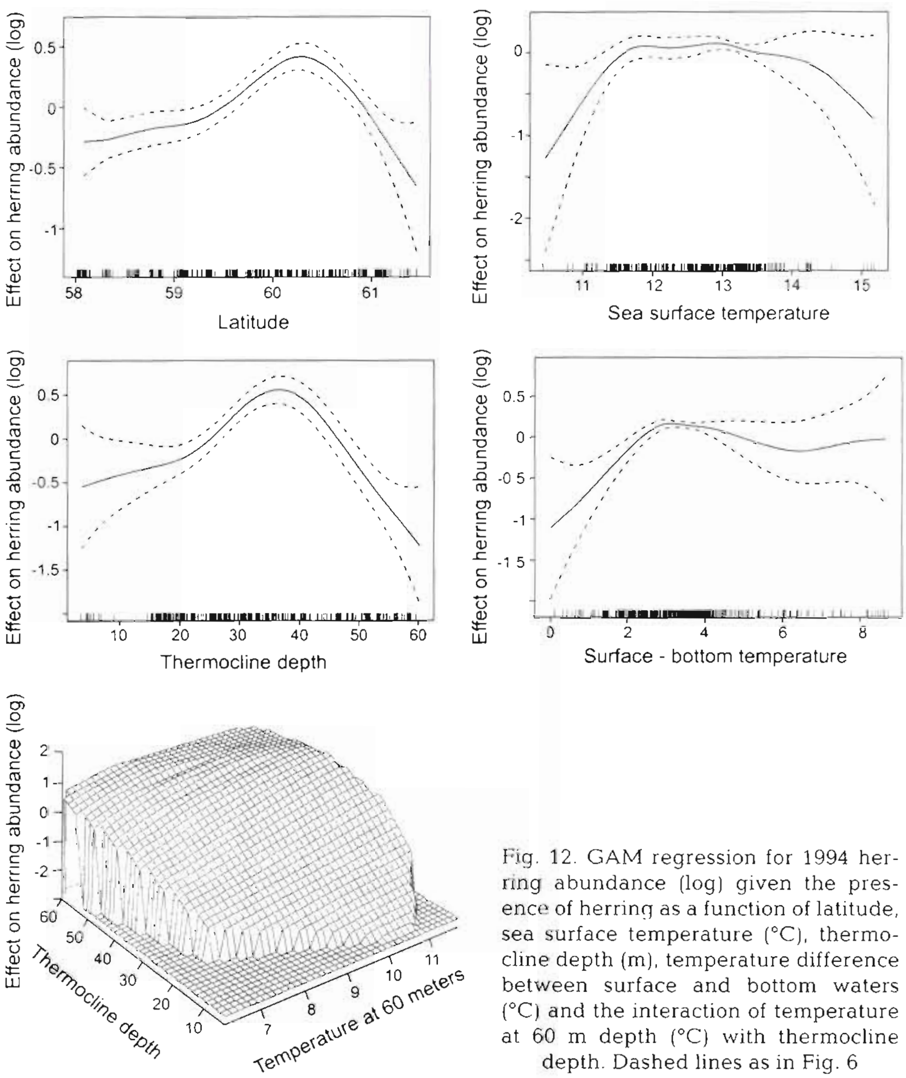

Fig. 12. GAM regression for 1994 herring abundance (log) given the presence of herring as a function of latitude, sea surface temperature (°C), thermocline depth (m), temperature difference between surface and bottom waters (°C) and the interaction of temperature at 60 m depth (°C) with thermocline depth. Dashed lines as in Fig. 6

ited in a shorter latitude range between 59.4° and 60.8° N and SST mainly lower than 12°C (second stage GAM). It needs to be underlined that the only spatial component found to be significant in the present study was the latitude. Therefore, the spatial dimension is restricted in a north-south geographic sense.

In 1994 and 1995 areas with the higher probability of finding herring present were south of 61° N with SST between 11 and 12.5°C. Given the presence of herring, in both 1994 and 1995 the abundance was greatest in the central part of the studied area (i.e. between 59° and 61° N, around the Shetlands), in waters with SST values around 12°C. Fish have the ability to perceive and select a limited thermal range in which they tend to congregate. This is usually the thermal range which offers them the opportunity for maximum expression of activity and is ultimately manifested in their abundance distribution. The influence of water temperature on fish behaviour is most pronounced prior to and during spawning. In all 4 years, the highest average prespawning herring abundances were mainly observed in SST between 11 and 12°C and to a lesser extent between 13 and 14°C. Prespawning herring abundance was, on average, greater in cooler surface waters in the south than in the north (Figs. 10 & 11). These SST values are characteristic of nutrient rich water of Atlantic origin and this may well account for the herring SST preferences.

Although temperature changes act as stimuli to fish, these changes may also indicate other changes in the environment, such as advective changes of water masses. In most cases temperature may serve as a useful indicator of the prevailing and changing ecological conditions. A current might affect the distribution of adult fish indirectly through the aggregation of fish food or by bringing about other environmental boundaries for them (e.g. temperature boundaries). In summer in the northern North Sea herring schools are

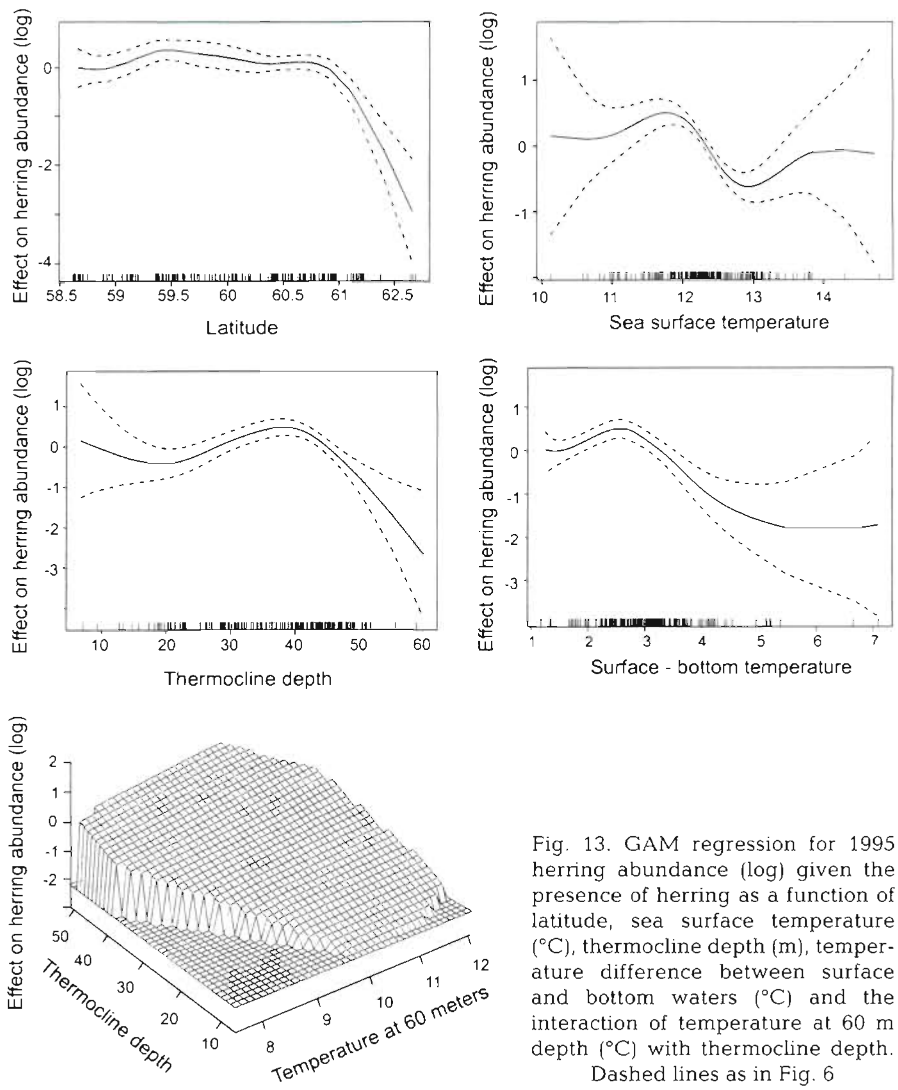

Fig. 13. GAM regression for 1995 herring abundance (log) given the presence of herring as a function of latitude, sea surface temperature (°C), thermocline depth (m), temperature difference between surface and bottom waters (°C) and the interaction of temperature at 60 m depth (°C) with thermocline depth. Dashed lines as in Fig. 6

feeding while moving towards their spawning grounds (Corten & van de Kamp 1992). Feeding schools are often associated with very productive waters, such as might be present on a particular bank (i.e. a shelf-break frontal zone), or at a boundary between 2 water masses (Laevastu 1993). In both 1994 and 1995, areas with the higher probability of finding herring present were located in transition zones between frontal and stratified waters (surface – bottom temperature values around 3°C). These waters also carried the highest herring abundances (second stage GAM). This can be seen as support for the previously proposed hypothesis that herring prefer these areas adjacent to mixing zones (Maravelias & Reid 1995, 1997).

It has been reported that in the central and northern North Sea, cold bottom water pockets can be found every summer; herring seemed to avoid these cold spots (Laevastu 1993). This was consonant with the findings of the present study: in both 1994 and 1995 increased difference between surface and bottom temperature values were associated with absence of herring (1-stage model) and lowest abundances (2-stage model). A reasonable scenario would be that areas with high surface – bottom temperature values are representative of more stratified waters (i.e. difference between surface and bottom temperature is high); primary (and hence secondary) production would then be expected to be relatively poor due to nutrient depletion leading to lower food supplies. Cold water pocket(s) were encountered during the surveys in the southeast part of the studied area (Maravelias 1997); herring tended to avoid these areas.

Herring is a pelagic species with daytime occurrence in layers below the thermocline, migration upwards to the thermocline during sunset, dispersion between thermocline and bottom during the night and aggregation close to the bottom during sunrise (Laevastu & Hayes 1981). Clearly, the diurnal migration of herring is influenced by the temperature gradient of the water column. Postuma (1957) demonstrated that at least 2 factors are involved in the pattern of diurnal migration of herring: light and temperature. He suggested that the pattern of the diurnal vertical migration of herring must be affected, both directly and indirectly, through the concentration of food at the thermocline. The areas with the higher probability of finding herring present were in waters with deeper thermoclines (>40 m, both 1994 and 1995) and temperatures at 60 m around 10°C (first stage GAM, only in 1994). Given the presence of herring, in both 1994 and 1995 the largest aggregations were found in waters with deeper thermoclines and temperatures at 60 m around 10°C (second stage GAM). Thus, both years showed increased average herring abundance for 60 m temperatures around 10°C and for deeper thermocline depths (up to 45 m). In the studied area in 1995, it was found that the regions with deeper thermoclines (>30 m) and temperatures at 60 m around 10°C carried zooplankton rich waters that were also associated with high average herring abundances (Maravelias & Reid 1997). In the northern North Sea ecosystem during summer, zooplankton starts its migration to deeper waters, where it hibernates. In July and August the thermocline becomes well established and *Calanus finmarchicus* (the main food of herring) moves deeper into cooler water beneath the thermocline (Lalli & Parsons 1993). It has been suggested that prespawning aggregations of herring follow the movements of zooplankton to deeper and cooler waters beneath the thermocline during summer (Maravelias & Reid 1997), and the present observations support this.

The present results clearly indicate that the 2-stage modelling approach conveyed additional insights into the ecological behaviour of herring in the area. The most significant aspect of this study is the pronounced similarity: (1) in the shape of the relationships between herring and environmental factors (revealed by the shape of the smooths) among years and (2) in the significance of these relationships with and without the zero observations. To a large extent this strengthens the belief that the observed relationships are authentic and characteristic of the stock. The temperature profile, the structure of the water column and the spatial location seem adequate to explain part of the observed relationships during the 4 year period, 1992 to 1995. Other factors not examined here, such as bottom depth and seabed substrate, may also be important. The modelled herring abundances show a strongly nonlinear dependence on the explanatory covariates. It is concluded that the herring are strongly influenced by the temperature based variability of the ecosystem and the presence of boundary zones enhancing local production and hence food availability.

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