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The effects of environmental factors on daytime sandeel distribution and abundance on the Dogger Bank

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ABSTRACT

Spring distribution and abundance of lesser sandeels during the day were linked to zooplankton densities, seabed substrate and various hydrographic factors using small scale empirical data collected in two areas on the Dogger Bank in 2004, 2005 and 2006. The results of a two-step generalized additive model (GAM) suggested that suitable seabed substrate and temperature best explain sandeel distribution (presence/absence) and that sandeel abundance (given presence) was best described by a model that included bottom temperature, difference between surface and bottom temperature and surface salinity. The current study suggests that suitable seabed substrate explains sandeel distribution in the water column. Bottom temperature and surface salinity also played an important role in explaining distribution and abundance, and we speculate that sandeels favour hydrographically dynamic areas. Contrary to our hypothesis sandeels were not strongly associated with areas of high zooplankton density. We speculate that in early spring on the western Dogger Bank plankton is still patchily distributed and that sandeels only emerge from the seabed when feeding conditions near their night-time burrowing habitat are optimal. The results also suggested that when abundance is over a threshold level, the number of sandeel schools increased rather than the schools becoming bigger. This relationship between patchiness and abundance has implications for mortality rates and hence fisheries management.

1. Introduction

The effects of shelf hydrography on the distribution and abundance of pelagic schooling fishes have been the subject of many studies. Some examples in recent literature are Pacific sardines in Mexico (Robinson et al., 2004, 2007), sprat and herring in the Gulf of Finland (Peltonen et al., 2007), European Anchovy off Spain (Drake et al., 2007), European anchovy and sardine in the Bay of Biscay (Petitgas et al., 2006) and herring in the northern North Sea (Maravelias, 1997) and there are many more. Solar heat, tide, wind and topography in shallow seas influence the development of spatially and temporally changeable areas of mixed and stratified waters and frontal zones (e.g. Bo Pedersen, 1994). These features can affect pelagic species distribution and abundance through a variety of mechanisms such as nutrient and plankton availability (see e.g. Cushing, 1989; Scott et al., 2006) as well as egg and larval dispersal (Proctor et al., 1998). The distribution of pelagic fish is however a complex phenomenon and in addition to oceanographic features, other factors such as seabed substratum can also play an important role (Maravelias et al., 2000).

Often considered a semi-pelagic species, lesser sandeels (*Ammodytus marinus*) spend most of the year buried in the seabed, only to emerge into the water column briefly in the winter and for an extended period in spring and summer. During a brief spell from November to January the sexually mature (mainly age 2+) sandeels enter the water column to spawn. The spring and summer months are the main feeding period and sandeels display a diurnal behavioural pattern where they emerge during the day to form large schools feeding on a variety of zooplankton prey, and bury themselves in the seabed at night. This strategy is probably adopted to conserve energy (Winslade, 1974a,b) and to avoid predators. The full extent of what triggers sandeel emergence from the seabed during the spring and summer, is not known but temperature, light intensity and food availability have been found to play an important role under laboratory conditions (Winslade, 1974a,b,c). During this pelagic stage growth rates increase rapidly (Bergstad et al., 2002).

When buried in the seabed, lesser sandeels require a very specific substratum (Macer, 1966; Reay 1970; Wright et al., 2000; Holland et al., 2005), favouring coarse sand with fine to medium gravel and low silt content. Bottom depth and bottom current flow also play an important role (Wright et al., 1998). These preferences have been attributed to the importance of both sediment permeability and bottom roughness for interstitial water movements to provide adequate oxygen supplies. The availability of this habitat was found to be strongly associated with the distribution of sandeels in the sediment

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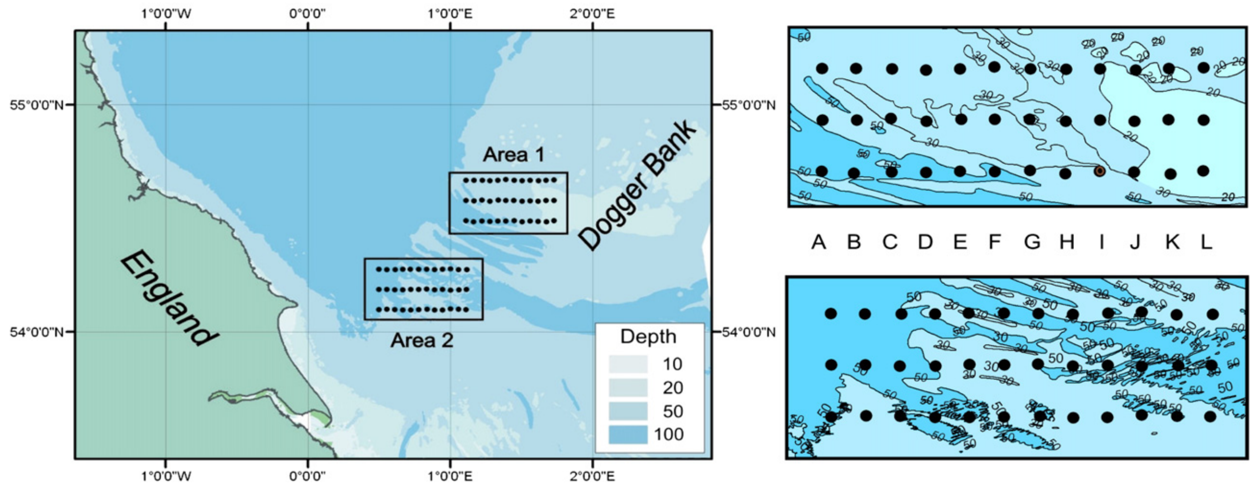

Fig. 1. Location of survey area showing the sample stations (●) and (right) detailed bathymetry maps of the two study areas. Each area consisted of a maximum of twelve approximately 18 km long transects A–L, 3.8 km spaced (see Table 1 for survey specific details). © British Crown and SeaZone Solutions Limited, 2007. All rights reserved. PGA 042007.005. "Not to be used for navigation".

in the northern North Sea and around Shetland (Wright et al., 2000; Holland et al., 2005).

Sandeels form an important trophic link between zooplankton and piscivorous predators and are also targeted by an industrial fishery. Although sandeels are preyed upon in the sediment (Hobson, 1986), it is more common when they are in transit to, or feeding in the water column. Here they are more readily available to a variety of mammalian, avian and piscean predators, and are under threat of pelagic trawls from the industrial fishery (Macer, 1966; Hobson, 1986; Engelhard et al., in press). In contrast to the well-documented characteristics of sandeel's seabed habitat, not much is known about the factors influencing sandeel distribution and abundance in the water column. This information is important for understanding and predicting the availability of sandeels to fisheries and predators (Frederiksen et al., 2007), by providing a better basis for spatially and temporally driven ecosystem-based management: Recent studies suggest that the North Sea lesser sandeels stock is divided into several reproductively isolated sub-stocks (Pedersen et al., 1999; Boulcott et al., 2007), which, in combination with spatially patchy fishing effort, makes them potentially vulnerable to local overexploitation.

Sampling sandeels in the water column using traditional methods such as trawls can be unreliable due to high variability in catches, particularly when abundance is low. Fisheries acoustics are often used in studies on pelagic fish species as they can provide a non-invasive, *in situ* insight into the species horizontal and vertical distribution in the water column. In this study we aimed to establish a qualitative relationship between acoustically derived data on sandeels in the water column and various environmental factors such as zooplankton, seabed substrate and hydrography using Generalized Additive Models. We hypothesise that sandeel distribution during the day is related to sandeel distribution in the seabed. As spring and summer are the main feeding seasons for sandeels we also expect sandeel distribution and abundance to be positively associated with areas of high zooplankton densities.

2. Materials and methods

2.1. Survey

The survey consisted of two areas in the southwestern Dogger Bank, central North Sea (Fig. 1). Area 1 covered an area known as the NW Riff, the western-most part of the Dogger Bank itself, and area 2, known as the Hills, was situated about 63 km southwest of area 1. Each area covered a maximum of approximately 800 km^2, with up to 36 sampling stations on regularly spaced North–South running transects. A total of three surveys were conducted in subsequent years each covering two weeks during spring and early summer (Table 1).

2.2. Sandeel data

Data on distribution and abundance of sandeel schools in the water column were collected using a calibrated dual frequency (38 and 120 kHz) splitbeam echosounder, stabilised for pitch and roll: a Simrad EK500 onboard the RV *Corystes* and an EK60 onboard the RV *CEFAS Endeavour*. Sandeels display strong diurnal behaviour patterns during spring (Freeman et al., 2004) so fisheries acoustic data were recorded during the morning from dawn until about 11:00 when the majority of sandeels were assumed to have entered the water column. Depending on the weather, the vessel steamed along transect with speeds of between 5 and 8 knots. To minimise temporal and spatial bias, each morning, two alternate transects were surveyed back to back (e.g. C and E), skipping one transect. After reaching the last transect, the remaining unsampled transects were surveyed in the opposite direction. Echograms from both frequencies were scrutinized and schools were selected using Sonardata Echoview's school detection module. Sandeel schools have a characteristic acoustic signature due to the absence of a swimbladder in this species. Their return echoes are less strong than those from clupeid schools (herring and sprat in this region) and produce a stronger signal on the high frequency (120 kHz) than on the low frequency (38 kHz) echograms. Sandeel backscatter was integrated (using 120 kHz data only at threshold of −65 dB) over 1 n.mi equidistant sampling units (EDSU) and biomass calculated using standard methods detailed in MacLennan and Simmonds (1992). Target strength (TS) values for sandeels were obtained from existing literature (see Mackinson et al., 2005) and validated with *in situ* TS measurements.

2.3. Zooplankton data

Each acoustic transect contained 3 sample stations, one at each end and one in the middle (Fig. 1). At each station a ringnet with 0.5 m radius (mesh 200 µm) and a mounted CTD profiler, measuring conductivity

Table 1
Surveys details

Year	Dates	Vessel	Transects	
			Area 1	Area 2
2004	19 April–5 May	*RV Corystes*	A–L	A–L
2005	6–18 May	RV *CEFAS Endeavour*	C–L	C–K
2006	10–19 May	RV *CEFAS Endeavour*	C–L	C–J+L

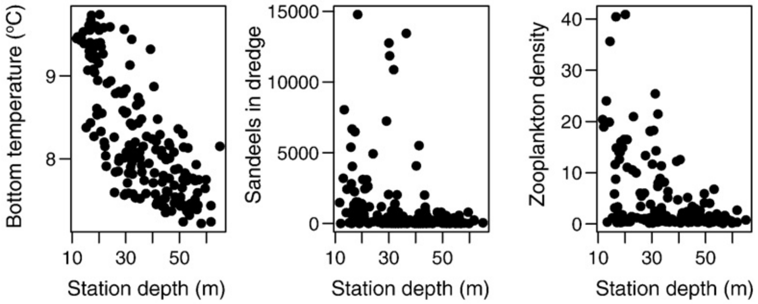

Fig. 2. Co-linearity scatterplots between covariates: temperature and depth; dredge abundance and depth; and plankton and depth.

(salinity), temperature and depth, were lowered to the seabed to sample the zooplankton community and hydrographic features simultaneously. All plankton samples were stored in buffered formalin and the zooplankton volume (in ml) was measured back in the lab. These volume estimations were converted to zooplankton densities by dividing the volume by swept area (ringnet aperture and depth sampled). To obtain information on the species composition, for each survey a selection of zooplankton samples were specified by taxa and counted. Apart from in 2004, this was done on the southern most stations of each transect of the northern area and the northern most stations of each transect of the southern area. In 2004 three stations per areas were selected, representative of shallow, medium and deep water; in area 1: 22, 32 and 41 m, and in area 2: 43, 50 and 61 m.

2.4. Hydrographic data

The upcast from the CTD provided vertical profiles of temperature and salinity on each station. Temperature and salinity at maximum depth of the CTD, which was mounted above the ring of the plankton net, 3 m above the seabed, and at 1 m below the surface were extracted. The differences between surface and bottom temperatures were calculated to assess the presence of any biologically meaningful thermocline. A temperature difference of 0.5 °C or greater between two water layers causes an increased difference in water densities which is necessary for phytoplankton to be able to increase production. This has been shown to have significant effects on the higher trophic levels in the North Sea (Scott et al., 2006).

2.5. Seabed habitat data

Information on suitability of seabed substrate for night-time sandeel burying habitat was inferred from a nocturnal dredge survey. Starting 2 h after dusk, sandeels in the seabed were sampled on each station by towing a modified scallop dredge for 10 min. All sandeels caught were counted and the catch was corrected for swept area. On a survey preceding the current study, seabed samples were taken using a Hamon grab. However as the Dogger Bank is thought to be topographically quite a dynamic region the sediment samples were not considered representative for the other surveys. The analysis of the sediment samples did confirm a preference of sandeels for substrates with low silt content (Holland et al., 2005). Given the evidence that the survey contained stations with, for sandeels, both suitable and unsuitable substrates, using sandeel abundance in the seabed at night as a proxy for suitable night-time habitat was thought, for the purpose of this study, to be more favourable than using sediment data. Even the most suitable seabed habitats can be unoccupied by sandeels when populations are below the area's carrying capacity (Holland et al., 2005).

2.6. Data analyses

The explanatory variables collected and available for analyses were bottom depth, bottom and surface temperature and their difference, bottom and surface salinity, zooplankton density and sandeel abundance in the seabed at night. We left out longitude and latitude because they were not considered ecologically meaningful variables in themselves. Any potential relationship found with these geographic variables would most likely be driven by underlying relationships in for example temperature or depth. The zooplankton density information was available for all the stations and was used for further analyses, whereas the sub-samples that where taxonomically scrutinized were used to provide additional insight between area and year plankton composition.

The explanatory variables were sampled on stations, as apposed to the acoustic sandeel densities, which were available on a 1.852 km (1 n. mi EDSU) resolution along each transect. We did not interpolate the explanatory variables along the acoustic transects, as it is based on

Table 2
Mean (variance) of on-station variables collected, by area and by year

Year	2004		2005		2006	
Area	1	2	1	2	1	2
Number of stations	36	36	30	27	30	27
Bottom temp.	8.37 (0.24)	7.56 (0.02)	9.25 (0.16)	8.01 (0.02)	8.71 (0.43)	7.65 (0.11)
Surface temp.	8.88 (0.13)	7.74 (0.14)	9.28 (0.15)	8.07 (0.05)	9.15 (0.13)	8.85 (0.29)
Mean temp.	8.56 (0.17)	7.59 (0.03)	9.27 (0.15)	8.03 (0.02)	8.87 (0.23)	8.00 (0.07)
Surface-bottom temp.	0.51 (0.18)	0.19 (0.08)	0.03 (0.00)	0.06 (0.01)	0.45 (0.41)	1.20 (0.47)
Bottom salinity	34.77 (0.00)	34.54 (0.01)	35.18 (0.00)	34.82 (0.01)	34.93 (0.00)	34.82 (0.00)
Surface salinity	34.76 (0.00)	34.54 (0.01)	35.18 (0.00)	34.83 (0.01)	34.91 (0.01)	34.74 (0.00)
Depth	30.69 (138.7)	47.27 (92.7)	30.35 (64.5)	47.91 (80.7)	30.01 (135.1)	48.54 (44.0)
Zooplankton density	0.91 (0.23)	1.10 (0.72)	16.32 (80.91)	7.93 (39.21)	0.70 (0.38)	1.09 (0.49)
Sandeels (dredge)	502 ± 178	134 ± 25	695 ± 187	290 ± 67	2263 ± 612	321 ± 136
Sandeels stat. (dredge)	63.9%	97.2%	80.0%	92.6%	96.7%	96.3%
Sandeels (acoustics)	212 ± 85	0	3583 ± 1347	449 ± 266	4244 ± 2972	241 ± 97
Sandeel stat. (acoust.)	33.3%	0.0%	63.3%	14.8%	86.7%	25.6%

Temperature (temp.) in °C. Sandeel abundance in numbers per 1000 m^2 ± standard error. Sandeel stat. represents percentage of stations with sandeels in the seabed at night (dredge) and acoustics (acoust.).

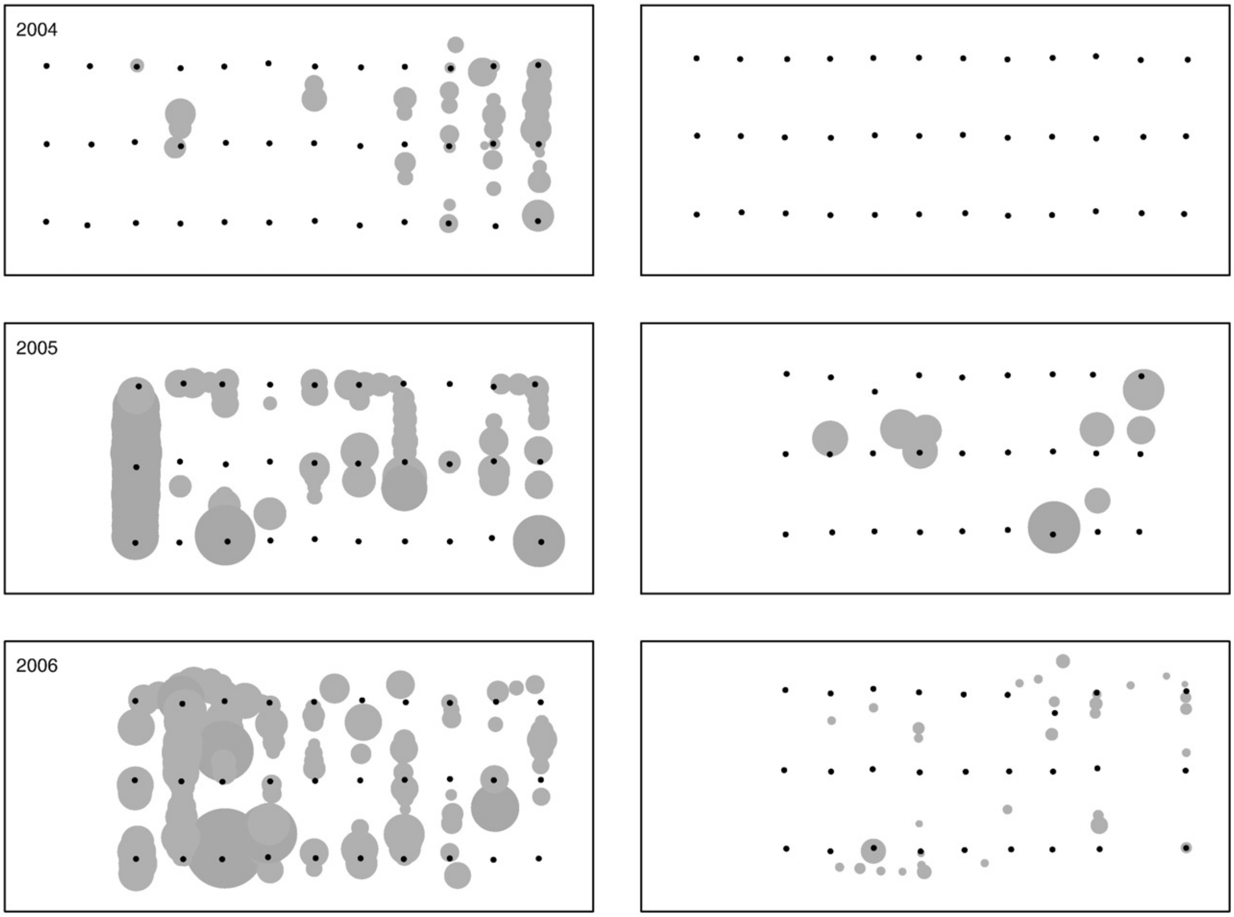

Fig. 3. Spatial distribution of sandeels in the water column in area 1 (left) and area 2 (right) for 2004, 2005 and 2006 (top to bottom). Area size of grey symbols proportional to densities (tons) per 1 n.mi equidistant sampling unit (equally scaled between years and areas). Location of sample stations is indicated by black dots (see also Fig. 1).

spatial autocorrelation, which goes against the assumption of independence as required for the multivariate analyses used in this study (see below). Furthermore, as interpolation is essentially averaging the data it would result in a "smoothed" and less accurate representation of the empirical on-station data before any analyses have taken place. This is particularly evident in small study areas. Similarly we did not use existing hydrographic models, because they were unlikely to achieve the high temporal and spatial resolution required for this study. Instead of interpolation, acoustic sandeel data along the transects were pooled by creating a 0° 3′ longitude and latitude rectangle around each station and combining the acoustic data within each rectangle for that station (between 1 and 4 EDSU observations per station). The size of the rectangle was chosen as a trade off between maintaining spatial high resolution and being large enough to incorporate at least part of the acoustic transect covered (to avoid absence of data), without overlapping with the next station. Although this method honours the authenticity of empirical data, it reduces the number of data available for multivariate analyses, so in this study data from the three surveys (years) were pooled. By combining the data we assumed that there was no behavioural difference between the three years, in relation to the independent variables used in the multivariate analyses (see below).

Data were visually explored with scatter plots displaying the relationship between sandeel density and all the studied variables. These relationships were then further examined and tested using generalized additive models (GAMs). GAMs (Hastie and Tibshirani, 1990) have become a well-established statistical tool in the last 15 years to describe, analyse and predict fisheries data (e.g. Swarzman et al., 1992; Maravelias and Reid, 1997; Maravelias et al., 2000; Kupschus 2003). A GAM is a flexible semi-parametric model used to determine the relationship between a response variable (sandeels) and explanatory variables, in this case the various environmental and year variables. It uses a link function to establish a relationship between the mean of the response variable and a smoothed function of the explanatory variable. In this study we used a cubic spline smoother. The level of smoothing is determined by the value of the smoothing parameters and in R software's "gam" package is determined by the degrees of freedom specified for the smoother. The least amount of smoothing is a straight line (1 *d.f.*) and the greatest is when the smoothed function explains the most variance: the smoother goes through all the points by allowing a separate gradient for each successive pair of points. The smooth function is usually not specified but is estimated nonparametrically from the data using a scatter plot smoother. The shape of the function is therefore determined by the data rather than being restricted to a parametric form (Hastie and Tibshirani, 1990). By increasing the

Table 3
Summary of mean numbers of plankton per group per area for each year

Cruise	2004		2005		2006	
Data	1	2	1	2	1	2
Number of stations	3	3	10	7	8	9
Calanus	570.60	664.10	612.26	4883.86	103.21	558.37
Temora	0.00	2.06	77.44	4.29	64.16	1.66
Copepods (other)	403.91	833.98	92.24	1434.16	121.42	371.01
Cladocera	9.23	2.06	20.66	0.00	1.30	13.62
Euphausids	0.00	2.06	17.42	10.20	0.00	0.71
Fish (eggs, larvae)	26.17	39.35	71.02	61.02	10.61	25.53
Chaetognaths	0.00	8.25	13.35	9.66	4.20	8.72
Plankton (other)	1818.68	210.50	16,579.73	1506.02	1216.49	428.55
Gelatinous	37.14	76.12	39.88	909.88	366.76	442.16

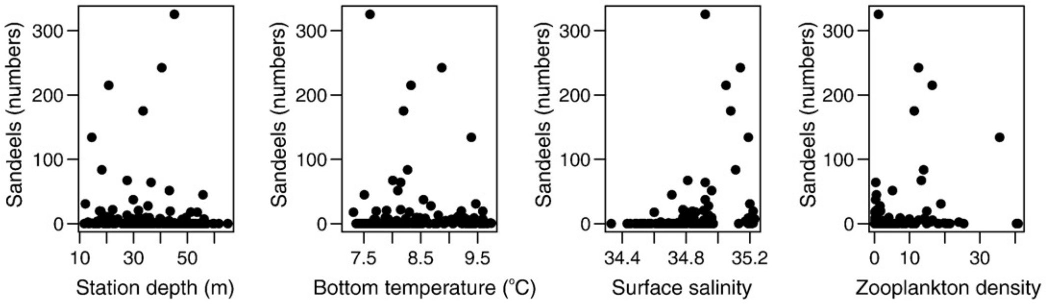

Fig. 4. Exploratory scatterplots between sandeel abundance in the water column and covariates depth, temperature, salinity and zooplankton density.

degrees of freedom, the smooth function becomes more flexible. The aim is to get the fewest degrees of freedom in the smoothers that will achieve the simplest model that meets all modelling objectives. This is the aim in most modelling exercises but particularly relevant in this study where the number of data points is relatively low. For more details on the methods we refer to the above papers.

The inter-correlation of explanatory variables is generally considered a problem in multiple regressions as it defies the requirement that covariates are independent. We therefore first created scatterplot matrices of the various explanatory variables to explore the existence of inter-relationships and selected only one of the two inter-correlated covariates for further GAM modelling. Co-linearity was most apparent between bottom depth and bottom temperature (Fig. 2) and depth was for that reason not used in conjunction with bottom temperature in the same model. The performance of both variables was tested in terms of their contribution to explain the variance in separate models and in every instance temperature was found to outperform seabed depth.

If some undetected inter-relationships were to remain present, Hastie's “gam” package in R divides this co-linear relationship with the explanatory variable equally between the two variables. In addition this package uses a backfitting algorithm that runs through the covariates and improves the overall smoothness at each iteration assuring that the order in which the covariates are defined in the model does not affect their contribution to the model in case of co-linearity.

Fisheries acoustic data often consist of high numbers of zero values, which usually makes them difficult to model. We therefore chose to apply a two-step model (Maravelias, 1999). In step 1 we modelled the presence and absence of sandeels in relation to the various covariates, and in step 2 we related sandeel abundance, given presence, to the covariates. Apart from statistical benefits, breaking the model up into two stages can provide a better ecological insight into the dynamics of the variables (Maravelias, 1999). The error structure of the step 1 model was expected to tend towards a binomial problem (fish present or not) and we used a logit link function. In step 2 the abundance data were highly skewed and all data were positive so we used a log link function and a gamma family (Wood, 2006).

To assess the performance of the models we combined a number of approaches: with high confidence in the empirical data, visual assessment of the ability of the model regression smoother to capture the general trend of the data points was considered very important, whilst aiming to keep the degrees of freedom as low as possible. Akaike's Information Criterion (AIC) was used for step-wise model validation. The significance ($p < 0.05$) of the covariates was used to assess the importance of the variable to the prediction of sandeel in the water column, but as GAMs use adaptive smoothing, these are not true p-values and were therefore only used as a relative measure of importance. The dispersed variables of sandeel abundance in the dredge (as a proxy for suitable seabed habitat) and zooplankton densities were square root converted to improve the spread of the data in the GAM regression.

It was decided *a priori* that year was to be included as a categorical variable, whether a year effect was found to be present or not. The purpose of this was to attempt to remove any temporal effects through multi-co-linearity with the other covariates and hence provide a better understanding of the contribution of the other covariates to explain the

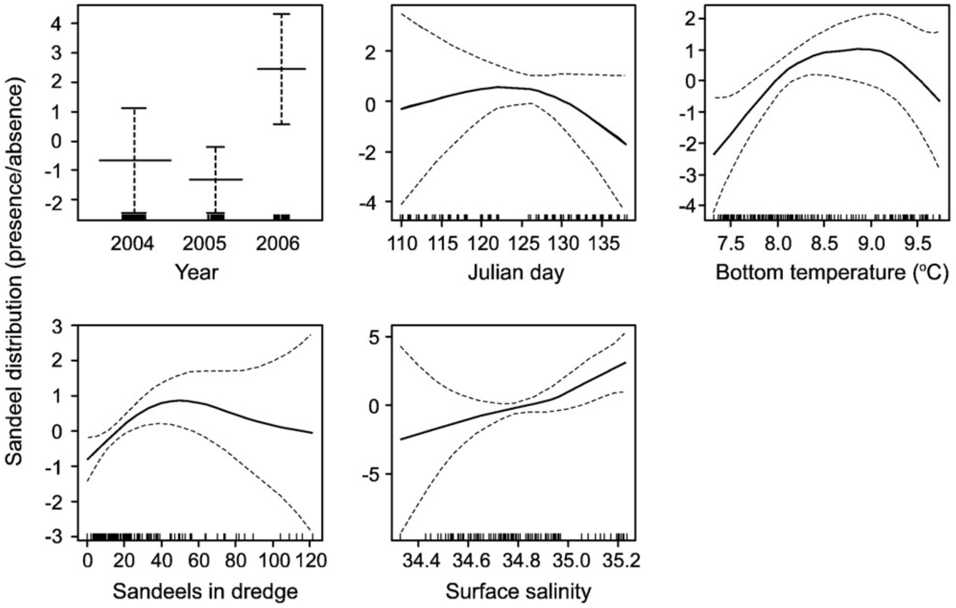

Fig. 5. GAM regression results of best step 1 model describing sandeel presence or absence (y-axes) as function of year, Julian day, bottom temperature, sandeel-dredge abundance and surface salinity. Each plot represents the effect of the specific variable on sandeel presence/absence, given the inclusion of the other explanatory variables. Dashed lines represent standard error ranges around the covariate main effects and tick-marks on x-axis represent location of data points. See Table 4 for summary statistics.

Table 4
Summary statistics of best step 1 model: sandeel presence/absence (see Fig. 5 for regression plots)

	d.f.	Chi square	*p*-value
Intercept	1		
Year	2		
Julian day	2	6.3945	**0.0114**
Bottom temperature	3	12.3520	**0.0021**
Sandeels in dredge (sq. rt)	2	7.6089	**0.0058**
Surface salinity	3	1.7707	0.4126

Null deviance: 231.85 on 172 degrees of freedom, residual deviance: 130.46 on 160 degrees of freedom, AIC: 156.46. Emboldened *p*-values are significant.

residual variance in the sandeel variables. The continuous variable Julian day was included for the same reason. GAMs also allow the inclusion of interactions between two covariates as a variable into the regression model. However, because the number of data points available in the study was relatively low, we were limited in terms of the number of variables we could use in the GAM regression as each added variable "costs" degrees of freedom. We therefore chose not to incorporate interactions. In consequence, the potential relationships found between the (single) independent variables in this study could be over-simplified as the addition of interaction between independent variables may have described more complex effects on the response variable.

3. Results

Sandeel numbers, derived from both acoustics and dredge, were highest in area 1 for all years and most sandeels were found in 2006 (Table 2, Fig. 3). The northwestern area 1 was on average shallower, warmer and more saline than area 2 (Table 2). Although in 2005 and 2006 the surveys took place during nearly the same 2-week period, 2005 had highest salinity and temperature readings in both areas. On an area scale, yearly stratification data were not consistent, both in terms of number of stratified stations and in terms of the magnitude of the difference between surface and bottom temperature. Only in area 1 in 2004 and in area 2 in 2006, mean difference between surface and bottom temperatures was higher than 0.5 °C. Some degree of stratification was present in both areas apart from in 2005.

The relative densities of zooplankton fluctuated between year and area (Table 2) and in 2005 plankton numbers for most groups were generally much higher than in the other two years. However the copepod species composition was relatively similar, with most *Temora* being found in area 1 and *Calanus* being most abundant in area 2 (Table 3). As the taxonomic composition was only analysed on three stations of each area in 2004 compared to between seven and ten stations for both areas in 2005 and 2006 we compared the variance in plankton composition between 2004 and 2005 and 2006. The variance of species composition was comparable between these years.

The exploratory scatterplots (examples in Fig. 4) showed several, largely non-linear, relationships between sandeel abundance and covariates. Some preferences for the medium to high temperatures and higher salinities were observed. No clear patterns existed with bottom depth with high sandeel numbers being found at most bottom depths apart from the deepest stations. As expected the bottom temperatures were highest on top of the shallow banks (Fig. 2).

The GAM models confirmed most of the trends that were apparent at preliminary exploration. After removal of time trends (year and Julian day) the best step 1 GAM model, describing sandeel distribution or presence/absence, was a function of bottom temperature (significant), suitable night-time habitat (numbers of sandeels sampled with a dredge, significant) and salinity (Fig. 5, Table 4). There was a significant increase in the chance of sandeel encounters in 2006 compared to 2005. Julian day also contributed significantly to the model. However the trend described by this regression is unclear due to the low confidence. Bottom temperature was the most significant explanatory variable showing that sandeels were most likely to be encountered in waters between 8.5 and 9.5 °C. A significant night-time habitat association was also detected with a larger chance of sandeel encounters during the day at (near) those locations where sandeels were found at night (square root converted). A decrease was observed at higher numbers. Although not significant, the covariate salinity was left in the model as it described some of the relationship with sandeel distribution and removing the variable deteriorated the model (based on the AIC score).

The best step 2 model, describing sandeel abundance given presence, included Julian day, bottom temperature, surface salinity (all significant), stratification and zooplankton (Fig. 6, Table 5). There was

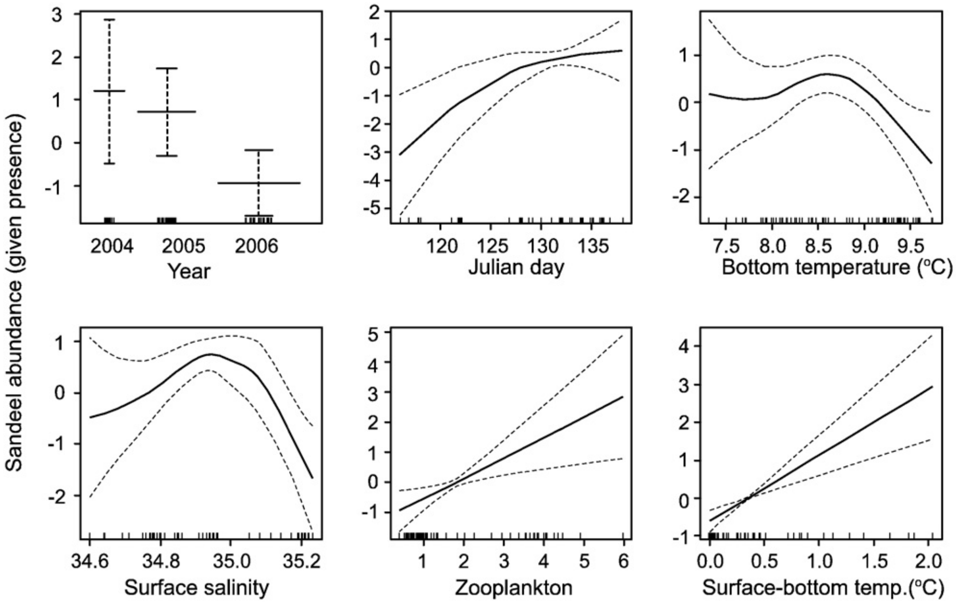

Fig. 6. GAM regression results of best step 2 model describing sandeel abundance given presence (*y*-axes) as function of year, Julian day, bottom temperature, surface salinity, plankton density and difference between surface and bottom temperature. Each plot represents the effect of the specific variable on sandeel abundance (given presence), given the inclusion of the other explanatory variables. Dashed lines represent standard error ranges around the covariate main effects and tick-marks on *x*-axis represent location of data points. See Table 5 for summary statistics.

Table 5
Summary statistics of best step 2 model: sandeel abundance given presence (see Fig. 6 for regression plots)

	d.f.	Chi square	*p*-value
Intercept			
Year	1		
Julian day	2	8.0835	**0.006261**
Bottom temperature	3	4.2237	**0.019676**
Surface salinity	3	6.5590	**0.002792**
Surface-bottom temperature	1	0.0827	**0.011653**
Zooplankton (square root)	1	0.2313	0.212651

Null deviance: 200.37 on 67 degrees of freedom; residual deviance: 80.36 on 54.87 degrees of freedom, AIC: 493.62. Dispersion Parameter for Gamma family taken to be 1.2656. Emboldened *p*-values are significant.

no significant difference in abundance between years on stations where sandeels were found. Given that sandeels were present, highest numbers were found with bottom temperatures of about 8.5 to 9.0 °C and at surface salinity of 34.9 to 35.0 ppt. Sandeel abundance increased linearly with increasing difference between surface and bottom temperature and although not significant, with increasing zooplankton densities. At higher plankton and surface-bottom temperature values the trend must be interpreted with caution as it shows a relatively large error in the fitted regression due to few data.

4. Discussion

In this study we set out to provide an in-depth, small scale and to our knowledge unique insight into the effects of the environment on distribution and abundance of the lesser sandeel in the water column during the early pelagic feeding stage on the Dogger Bank. We found that sandeel distribution in the water column was explained by availability of suitable night-time seabed habitat and medium to high bottom temperatures. Similar bottom temperatures, high surface salinity, stratification and to a lesser (non-significant) extent zooplankton, positively affected the abundance in areas where sandeels where present. A two-step GAM model has limited use in predictive mode, as it is more complicated to apply than a single model. This two-step modelling approach was primarily used as an attempt to deal with the difficulties of modelling overdispersed data, such as often found in fisheries acoustics. The first step aimed to link the hydrographic and seabed variables that drive the distribution of sandeels and the second step determined the abundance of sandeels given that they are found at a location. It was not the aim of this study to use GAMs in predictive mode and although the quantitative results need to be used with caution, it did prove a useful tool to identify the environmental variables driving sandeel distribution and abundance in the water column and to describe the multiple, often non-linear trends between the variables.

The results of this study show a clear relationship between sandeel distribution in the water column and abundance to bottom temperature with an optimum between 8.3 °C and 9.0 °C. Laboratory experiments recording activity at 5, 10 and 15 °C intervals suggested that sandeels become markedly more active (i.e. emerged from seabed and swimming in the tank) at 10 °C (Winslade, 1974c), which supports the results of this study. At the highest recorded temperatures a slight decrease in the chance of sandeel presence was observed and lower sandeel abundance (given presence). We also found a preference to saline water, with highest numbers of sandeels found in waters of between 34.9 and 35.0 ppt. The Dogger Bank is an area influenced by saline shelf water (Otto et al., 1990) as well as more fresh water from river outflows (Munk et al., 2002). The mean salinity from area 1 was consistently higher than that of the southwestern area 2, which may suggest that they were positioned in proximity of or at the boundary between the two water masses.

Sandeel abundance was found to be positively related to an increasing difference between surface and bottom temperature suggesting that they favour more stratified waters. However the maximum observed difference was only small (≤~2.5 °C) and suggests that the timing of the survey periods occurred near the onset of stratification, which is known to take place in the deeper (>50 m) parts of the central North Sea due to insufficient tidally generated energy (e.g. Riepma, 1980). Both thermal (Brown et al., 1999) and haline fronts (Munk et al., 2002) have been reported in and near the study area and although this survey was too early in the year for these fronts to have developed, it is likely that they are of significance to sandeel ecology. An association with frontal areas is a common feature for many planktivorous fish species (e.g. Maravelias, 1997; Maravelias and Reid, 1997; Zamon, 2003; Robinson et al., 2007), and is particularly evident at larval and juvenile stages (e.g. Munk, 1993; Munk and Nielsen, 1994; Nielsen and Munk, 1998), including pre-settled sandeels (Munk et al., 2002).

Seabed depth could not explain the distribution or abundance of sandeels in the water column, which is probably due to both survey areas being within the sandeel optimal depth range of 30–70 m (Wright et al., 2000). However more sandeels were found in the seabed in shallower stations and a strong negative linear relation between bottom depth and temperature was apparent. This suggests that bottom temperature has more of a direct effect on sandeel distribution and that depth covaries with bottom temperature.

In 2006 the chance of sandeel encounters in the water column was significantly higher than in 2005, but the abundance within the areas where sandeels were present was not significantly different. Although this applies only to 2005 and 2006, it would suggest that in years of higher sandeel abundance (Table 2) schools do not become bigger but the number of schools, i.e. the patchiness increases. Capelin in the Barents Sea also showed a positive relationship between abundance and patchiness on both large (200–300 km) and small (70 km) spatial scales (Fauchald and Erikstad, 2002). The opposite was found in a study on herring, sprat, anchovy and sardines, which concluded that no relationship existed between abundance and number of schools or clustering of those schools. This result was interpreted by the fact that the population abundances were not at extreme levels and would therefore not have been a forcing parameter on the spatial aggregation of schools (Petitgas et al., 2001). Our findings suggest that for sandeels, stock size does have an effect on aggregative behaviour and would imply that sandeel abundance was over a threshold level. However it is difficult to draw any solid conclusions as our survey was on a small temporal and spatial scale. Relationships between patchiness and abundance have implications for fisheries management, as increased patchiness enhances the possibility of encounters with both natural predators (e.g. seabirds, see Fauchald and Erikstad, 2002) and the commercial fishing fleet and hence affects mortality of the species.

The results of this study confirmed the hypothesis that sandeels in the water column remained within a few kilometres of suitable burrowing seabed substrate during the day. The site fidelity of the lesser sandeel to its night-time seabed habitat may be largely explained by the absence of a swimbladder. This makes them relatively poor swimmers such that they would incur high energetic costs for longer range foraging. The regression plot of suitable seabed habitat (night-time sandeel abundance in dredge) suggested that with more sandeels in the seabed, the chance of sandeels being present in the water column first increased and then reached an asymptotic level. At the highest numbers of sandeels in the seabed, the relationship with daytime sandeel presence became negative. We ignored this part of the regression, as the confidence was low. Not much is published on whether adult sandeels return to the same burrowing site or more generally, on the range of daily sandeel movements. Tagging experiments in Shetland and Orkney revealed that adult *A. marinus* is capable of travelling distances of many tens of kilometres but all recaptures were in the following one to three years (Gauld, 1990). Underwater observations on sandeels in the Baltic showed a daily movement between their burrowing site in shallow waters and deeper water 1 km away (Kühlmann and Karst, 1967). This scale of movement fits with the findings of the current study where the size of the spatial rectangles around each station was three minutes longitude by three minutes latitude, covering ~18 km^2. Sandeels on the Dogger Bank have been reported to aggregate in dense schools at the edge of the banks, a behaviour that the commercial fishing fleet utilizes by fishing along the 30–40 m isobaths (Mackinson and van der Kooij, 2006). The current results suggest that sandeels on the Dogger Bank make daily movements of up to 5 km from their burrowing sites, largely situated on top of the shallow banks, to deeper waters off the bank. Commercial sandeel catches had previously been found to spatially overlap with the distribution of those seabed substrata favoured by this species (Wright et al., 2000) and this study confirms that indeed the distribution of the night-time habitat can be used as a proxy for sandeel distribution in the day.

The lesser sandeel is a planktivorous species emerging from the seabed in spring to feed, so we expected zooplankton to have a strong effect on sandeel distribution and abundance. However the results showed no relationship between zooplankton density and sandeel distribution (presence/absence). In areas where sandeels were found, their abundance was positively related to zooplankton densities, albeit non-significant. This suggests that at this time of year, availability of suitable seabed substrates is the more important factor driving sandeel distribution and that the highest sandeel densities tended to be found in the water column at those favourable seabed locations where zooplankton concentrations were also high. During spring and summer sandeels need to increase body condition to survive the winter and to be able to produce gonad tissue for spawning (Greenstreet et al., 2006). This is achieved by increasing calorific intake through feeding whilst keeping metabolic expenditure at a minimum. In laboratory conditions the presence of zooplankton in the water above the seabed where sandeels were buried, triggered them to emerge, suggesting that they have the ability to detect prey (Winslade, 1974a). When local feeding conditions are sub-optimal, the costs involved with foraging expeditions further a field will at some point outweigh the benefits of (uncertain) energy gain. This effect of lower trophic level abundance on sandeel behaviour is corroborated by Greenstreet et al. (2006) who found that annual changes in timing of the spring bloom relative to their survey affected the recorded sandeel biomass in the water column. Apart from energetic costs an important additional factor is that the prolonged time spent in search for food will increase the risk of predation. This suggests that in early spring when zooplankton biomass is not yet at its peak and maybe more patchily distributed, sandeels only emerge from the seabed when conditions near their night-time habitats are favourable. We speculate that the formation of thermal-haline fronts later in spring would provide more predictable and therefore reliable foraging conditions, due to high concentrations of zooplankton associated with these sites. It is worth noting that the different components of the sandeel population spend different amounts of time in the water column (Bergstad et al., 2002). To survive the winter the early life stages, particularly age 0 but also age 1, need to increase their body condition to a larger extent than the age 2+. This suggests that the younger sandeels cannot afford to wait for optimal local feeding conditions and are therefore more likely to enter the water column in search for food and to spend more time foraging. As we had no information available on the age composition of the sandeel schools we could not test these hypotheses with the current data set. However it is likely that this age-dependent behaviour contributed to the poor significance of the relationship between sandeel abundance and zooplankton.

Other factors that could have had an effect on sandeel distribution and abundance and were not incorporated in this study are competitors and tidal states. Herring and particularly sprat, both found in the area, have a similar zooplankton diet. However, their diurnal behaviour is different and sprat were observed to be more active in the water column during the night at this time of year. It is therefore unlikely that it had a direct impact to our study. We aimed to reduce the effect of time of day by surveying for sandeels only during the morning but we did not account for tidal state. Tidal speed and direction could affect sandeel distribution and abundance in at least two ways. Sandeels are likely to use tidal currents to move horizontally in the water column as it would conserve energy. This would allow them to move further from their burrowing sites, spending less time in the water column than by actively swimming alone. Although this is likely to have played a role, the spatial link between sandeel distribution in the water column and in the seabed suggests that the daily vertical movements in this study were largely within 18 km^2. Tidal state could also have impacted through a mechanism described as the tidal coupling hypothesis (Zamon, 2003 and references therein). This concept suggests that in habitats with strong jets and currents, foraging behaviour of piscivorous predators is strongly associated with tidal current. Spatially predictable currents create changes in zooplankton distribution and abundance and attract zooplanktivorous fish aggregations. These in turn attract piscivorous predators. A link between tidal current and distribution of planktivorous fish was confirmed for Pacific sand lance, a species related to the lesser sandeel, but not with fish densities (Zamon, 2003). Tidal currents in this area of the Dogger Bank are relatively weak (≤1 knot) and strong jets were not expected to occur until the formation of fronts later in the season.

This study confirms that the daytime distribution of sandeels in the water column is linked to the location of suitable sediments, which they use to bury themselves in at night. In combination with the specific water column habitat requirements highlighted here, the availability of this particular substratum will limit their distribution. However this unique diurnal behaviour does also confer a particular advantage in that it offers a refuge from predators, including commercial fisheries. This is of particular importance if part of the stock remains submerged, since it ensures that some fraction of the stock is unavailable to predators. Such a behavioural trait can be key to the long-term resilience of this species. These findings could also contribute to improving management of the various North Sea sandeel stocks, for example by identifying more accurate spatial and temporal boundaries of closed areas for fishing (Greenstreet et al., 2006). Although not apparent for the Dogger Bank area, the potentially large effects of tidal currents on the daytime distribution of sandeels are still poorly understood, so future work on this aspect of sandeel ecology is recommended.

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