

**Spatial modelling of spawning habitat suitability for the sole (*Solea solea* L.) in the eastern English Channel and southern North Sea**

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**Abstract**

The quality and quantity of suitable spawning grounds and nursery areas is thought to represent one link in the chain of physical and biological factors that influence annual levels of recruitment in flatfish populations. Despite the growing body of literature describing fish-habitat relationships and variations in habitat quality, there are limited examples where the results are subsequently used to describe and map spatial variations in both habitat quality and quantity. Here we outline an approach to developing models of spawning habitat suitability for sole (*Solea solea* L.) in the eastern English Channel and southern North Sea, using data on the distribution of sole eggs in relation to temperature, salinity, depth and sediment type. Raster maps of the environmental variables, developed within a Geographical Information System (GIS), form the basis of the habitat models. Monthly spatial variations in sole egg abundance are modelled using regression quantiles, a distribution-free regression technique that provides linear model estimates for any part of a biological response distribution, and therefore affords greater flexibility to modelling species-habitat relationships. The regression quantile parameter estimates are then used to re-code the environmental raster maps to produce maps of habitat suitability. The final habitat models depict both temporal and spatial variations in spawning habitat suitability for a single spawning season.

Keywords: Habitat suitability models, sole, Geographical Information Systems, regression quantiles, eastern English Channel, southern North Sea

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## **Introduction**

A number of studies examining both the level and variability of recruitment in flatfish have provided evidence in support of the ‘nursery size hypothesis’ (Van der Veer *et al.*, 2000), whereby a positive relationship has been demonstrated between both the level of recruitment (Rijnsdorp *et al.*, 1992) and the abundance of juveniles (Gibson, 1994) with the quantity of nursery habitat available. However, habitat quantity cannot be considered in isolation from habitat quality as both will act interdependently to influence the growth and survival of fish throughout their life history. The availability of suitable habitat would therefore be expected to place controls on the level of recruitment in flatfish populations (Gibson, 1994). In principle the same may also be true for other stages and events that define the recruitment process, such as the degree of spawning activity.

In considering areas of future research into flatfish recruitment, Rijnsdorp *et al.* (1995) highlighted the need for increased awareness into the habitat requirements and characteristics of both pelagic and demersal life history stages. In attempting to address this issue, the response of a species life stage to the range of habitat factors encountered needs to be assessed, with models developed that provide estimates of the response (e.g. biomass, density) according to the spatial and temporal variations in the underlying habitat variables. Unfortunately the entire range of variables that may quantitatively define and describe habitat are largely unknown, and as a consequence models generally need to rely on a few, relatively simple to measure, abiotic descriptors (Brown *et al.* 1997).

In this study we develop models that describe both temporal and spatial variations in spawning activity for the sole (*Solea solea* L.) in the eastern English Channel and southern North Sea, using digital maps of physical habitat descriptors as the basis for the habitat models. Within this region sole have been found to spawn predominantly within more inshore waters and over offshore sandbanks, at depths of less than 30 m (Borremans, 1987; Van der Land, 1991; ICES, 1992; Grioche, 1998).

## **Materials and Methods**

### **i. Survey Data**

Data on the temporal and spatial distribution of sole eggs within the eastern English Channel and southern North Sea were collected by the UK Centre for Environment, Fisheries and Aquaculture Science (CEFAS) as part of an internationally co-ordinated survey covering the eastern and western Channel and southern North Sea during 1991 (Figure 1). Surveys took place in March, April, May and June to coincide with the peak spawning period, with survey stations located on a spatial grid corresponding to ICES grid squares and subdivisions thereof. Both the number of stations and the spatial coverage varied during each survey. Details of the sampling methodology used are given in ICES (1992). Stage 1a sole eggs were taken as representative of the location of spawning adults, being at most 2 days old in ambient temperatures of 7 °C (Riley, 1974). Temperature and salinity profiles were also taken at each station.

Chart depth and sediment type at each survey location were obtained directly from charts and maps developed and supplied by the UK Hydrographic Office (UKHO) and the British Geological Survey (BGS). Sediment type was represented as either one of 15 sediment classes based on Folk (1954), or of three classes located along the French coast of the eastern Channel, generalised by the BGS from ‘Les sédiments superficiels de la Manche’ published in 1979 by the Bureau de Recherches

Géologiques et Minières (BRGM), the Centre National pour l'Exploration des Océans (CNEXO) and the Service Géologique National (SGN).

## ii. Modelling spatial variations in the abundance of sole eggs

The approach taken to develop the predictive models for spawning sole was dependent on the type of data representing the habitat variables. For depth, temperature and salinity, monthly estimates of changes in stage 1a sole egg abundance were made using regression quantiles (Koenker and Bassett, 1978). For sediment type represented as categorical data, differences between the median stage 1a egg abundance associated with each sediment type were examined.

Regression quantiles extend the concept of one-sample quantiles to the linear model by minimising a function of absolute deviations, in contrast to least-squares regression which minimises a function of squared deviations. The 50<sup>th</sup> regression quantile is equivalent to a least absolute deviation (LAD) regression where 50% of the observations are less and 50% greater than the fitted line. LAD regression therefore estimates the conditional median in a linear model, as opposed to ordinary least-squares regression which estimates conditional means. Regression quantiles are therefore distribution-free and consequently require minimal assumptions as to the form of the error distribution (Cade *et al.* 1999).

Regression quantiles also offer additional advantages over least-squares regression in being able to provide estimates throughout the range of the response distribution. Predictive models are therefore not restricted to central estimates alone, but can be developed for a range of quantiles, including near the upper limits of the response. Thomson *et al.* (1996) call for the use of such methods to provide estimates of the upper limits imposed by the measured habitat variables. They argue that changes near the upper limits of a response would be expected if the measured variable were the active limiting factor, with the variation below the maxima caused by interaction with unmeasured variables. Predictive models based on upper estimates of the species response can therefore account for unmeasured ecological factors, whilst also allowing response estimates to be made for data that fails the assumptions imposed by least-squares regression; a common feature of ecological data (Terrell *et al.* 1996; Thomson *et al.* 1996; Cade *et al.*, 1999).

A range of regression quantiles were examined (e.g. 10<sup>th</sup>, 25<sup>th</sup>, 50<sup>th</sup>, 75<sup>th</sup>, 80<sup>th</sup>, 85<sup>th</sup>, 90<sup>th</sup>, 95<sup>th</sup> and 99<sup>th</sup>) in order to determine a model of best fit for both central (50<sup>th</sup>) and upper quantiles. An initial investigation found that parameter estimates based on  $\log_e(y + 1)$  transformed stage 1a egg data gave a better fit to the data points. Regression quantile models were therefore developed for transformed data and subsequently back-transformed to the original units when developing the final habitat models. The three variables of depth, temperature and salinity were initially included in each quantile model, with the best set of predictors chosen through backwards elimination. The significance of each variable was determined through hypothesis testing of the full model against a reduced model where the parameter being tested was constrained to zero. *P*-to-remove was set at 0.05. The testing procedure used an asymptotic rank-score test statistic developed by Koenker and d'Orey (1994), with probabilities evaluated with a  $\chi^2$  distributed with the appropriate degrees of freedom (1 for each parameter being tested). Once the predictors had been selected, all first order interactions were included and again tested for significance through the construction of hypothesis tests. Estimates were made for both central models and the highest quantile model with significant slope coefficients, in order to provide the best estimate of changes in the response variable(s) at the upper limits of the distribution. The computer program BLOSSOM (Slauson *et al.*, 1991) was used throughout this study to develop regression quantile estimates and construct hypothesis tests. The reader is referred to Cade *et al.* (1999) for a more detailed description of the statistical theory of

both regression quantile estimates and the rank-score hypothesis test implemented within the BLOSSOM program.

As sediment type data was only available for approximately two-thirds of the survey stations, and as the data was represented by two different classification systems, a separate approach had to be taken to determine whether the distribution of sole eggs was related to sediment type. Using the available data, the difference in sole egg abundance ( $\log_e [y + 1]$  transformed) between the different sediment types was examined. As each type was associated with a limited number of observations, sediment types were first aggregating into four classes. These were; > 80% gravel, between 30 and 80% gravel, between 5 and 30% gravel, and < 5% gravel. Percentage content of gravel was used, as opposed to sand or mud, as it was common to both classification systems represented on the BGS maps.

### **iii. Development of Digital Environmental Maps**

Digital raster maps, or layers, were created within the GIS (ArcInfo 7.2.1, Environmental Systems Research Institute, USA) for bathymetry, sediment type, mean water column temperature and mean water column salinity. To develop each raster layer, the raw data had to be entered initially into the GIS either as a series of vector points, polylines or polygons, depending on the data type, and referenced to the same underlying co-ordinate system. The vector data were then converted into a raster format using the techniques described below. Raster data formats facilitate spatial modelling by allowing new raster layers to be calculated based on the values of the spatially coincident cells within the input layers. Here, the input layers were the environmental variables with the output layer the habitat suitability maps.

To create a bathymetric raster map, contours and spot depths were digitised as a series of points and vector polylines from UKHO charts covering the study region. Interpolation of the vector data into a raster layer of continuously varying depth was achieved using a modification of a discretised thin plate spline routine, and implemented in ArcInfo, which permits the fitted model to follow abrupt changes in terrain. The quality of the interpolation procedure was evaluated by withholding 2% of the data points from a subset of the data, and calculating the root mean square (RMS) error of the difference between the original data points and the interpolated, spatially-coincident raster cell. The surface was also inspected visually, with small surface anomalies modified by increasing or decreasing the data point density within the surrounding area. After each modification, the interpolation procedure was re-run, and the whole process repeated until a more representative surface was obtained. A cell size of 200 m<sup>2</sup> was chosen for the final raster map.

Monthly temperature and salinity values from the 1991 sole egg survey were digitised and represented in the GIS as a series of vector point layers. Interpolated raster surfaces were produced using minimum-curvature splines to ensure the output surface conformed to the input points with a minimum of error. Other exact interpolation techniques were explored (e.g. kriging) and found to produce similar results, with the final technique selected based on the lowest RMS error obtained using a similar methodology to that described above. Output raster layers of 200 m<sup>2</sup> cell size representing mean water column temperature and salinity were produced for each month.

A digital map of sediment types was developed from BGS 1:250 000 scale paper maps by digitising sediment regions as a series of contiguous vector polygons. The BGS map series adopts the Folk (1954) classification system and individual polygons were coded accordingly. On the French side of the eastern Channel, sediments classes were generalised by the BGS from 'Les sédiments superficiels de la Manche (1979)'. Additional secondary qualitative sources of information were

used to complete areas of the map where data were missing. These areas were principally close to the British coastline and on the eastern side of the Dover Straits. Data for a large region of the Belgian coastal zone were also missing, and as no secondary sources of information were available, the region was broadly classified according to the predominant sediment types found within the surrounding area, namely sand, slightly gravelly sand and gravelly sand. The final sediment map was converted from the vector polygons into an integer raster layer of 200 m<sup>2</sup> cell size, with each cell holding the relevant sediment code in its attribute table.

#### iv. Habitat Suitability Models

A diagrammatic summary of the methodologies employed to develop the habitat models is given in Figure 2. In Step 1, parameter estimates from the highest significant regression quantile for each month were used to re-code the cells in the relevant environmental raster maps. This produced a single prediction surface of sole egg abundance for the three continuous variables of depth, salinity and temperature. The sediment type raster layer was also re-coded using the 95<sup>th</sup> percentile of sole egg abundance determined for each sediment class. The final habitat suitability map for each month was calculated as the geometric mean of spatially-coincident cells in the two input layers (Step 2). The geometric mean is commonly used to ensure that regions considered unsuitable in relation to one or more variables are classified as zero regardless of the suitability at that location of other variables in the model (Brown *et al.*, 1997). To produce an overall habitat suitability map for the entire spawning season, the four monthly sole egg prediction models were initially scaled from 0 to 1 to ensure that each month was given equal weighting in terms of the relative importance of the habitat. The final habitat model was calculated as the arithmetic mean of spatially-coincident cells for the four monthly raster layers of predicted relative sole egg abundance (Step 3).

The entire process was repeated for the monthly prediction models developed from the central (50<sup>th</sup>) regression quantile parameter estimates and median sole egg abundance within each sediment class in order to assess potential differences between a model based on central estimates of the species response with one based on the equivalent upper estimates. To simplify visualisation, the final habitat models were re-classified into a map consisting of four classes ranging from 0 representing unsuitable habitat, to 1 representing optimal habitat. These were 0 to 0.25, 0.25 to 0.5, 0.5 to 0.75, 0.75 to 1.0. The ability of the final habitat models to predict changes in sole egg abundance as a factor of spawning habitat suitability was evaluated using data on the spatial distribution of sole eggs along the French coast of the eastern English Channel during April 1995 (Grioche, 1998).

## Results

The spatial distribution and abundance of stage 1a sole eggs from March to June 1991 is shown in Figure 1 with a summary of the results used to develop the regression quantile models provided in Table 1. Of the four months the abundance was generally highest in April, with a mean egg abundance of 4.7 m<sup>-2</sup>. Within each month egg densities were generally highest within the more inshore regions and along the French and English coasts. The mean water column temperature gradually rose from 7.7 °C in March up to 11.3 °C in June, whilst the mean water column salinity remained relatively constant.

The regression quantile models developed for each month are described in Table 2 and shown in Figure 3. In March both temperature and depth were significant for quantiles greater than the 50<sup>th</sup> (min.  $P < 0.05$  for all quantiles) with a significant interaction found between depth and temperature for the 50<sup>th</sup> and 94<sup>th</sup> quantiles ( $P < 0.05$ ). The 94<sup>th</sup> quantile therefore gave the highest estimate of changes expected in the abundance of sole eggs when both depth and temperature are the active

limiting factors. Egg abundance was found to be higher within the warmer, shallower regions of the eastern English Channel and southern North Sea, with the 50<sup>th</sup> and 94<sup>th</sup> regression quantile models predicting a positive abundance of eggs at temperatures above 6.35 °C and 5.35 °C respectively at a depth of 10 m below chart datum.

For April, depth and salinity were found to be significant for the 55<sup>th</sup>-79<sup>th</sup> quantiles ( $P < 0.05$ ). Removal of either term led to the remaining term becoming non-significant, indicating the weakness of a model containing only a single parameter. As a result the 50<sup>th</sup> quantile could not be estimated. Both models predicted higher egg abundance within the shallow water regions, and also with increasing salinity.

In May temperature and salinity were found to produce the model of best fit for the 84<sup>th</sup>-88<sup>th</sup> quantiles, with a temperature-salinity interaction also significant ( $P < 0.05$ ). In contrast, temperature and depth produced the model of best fit based on central estimates. For the upper model, egg abundance decreased with temperature at higher salinities, but predicted a slight increase with temperature at lower salinities. Egg abundance decreased with salinity at all temperatures. For the central model, a negative relationship was found between egg abundance and both temperature and depth. In June both temperature and depth were found to produce the model of best fit for a few upper quantiles (80<sup>th</sup>-87<sup>th</sup>), with the 87<sup>th</sup> quantile the highest where both terms were significant, along with the interaction between temperature and depth (min.  $P < 0.05$ ). For the central model depth alone proved to be a significant predictor ( $P < 0.01$ ), with egg abundance decreasing with depth, similar to all other models where depth was included as a significant explanatory variable.

An overall significant difference was found between the abundance of sole eggs associated with the four sediment classes (Kruskal-Wallis,  $P < 0.05$  for all four months), but not between all individual classes. As a result the classes were further aggregated based on the least significant differences in sole egg abundance between the previous four classes. The two final sediment classes were  $> 30\%$  gravel, and  $< 30\%$  gravel (Figure 4). Significant differences in egg abundance between the two sediment classes were found for all months (March, Mood's  $\chi^2_{(1)} = 20.84$ ,  $P < 0.001$ ; April, Mann-Whitney  $W = 446$ ,  $P < 0.001$ ; May, Mann-Whitney  $W = 567$ ,  $P < 0.001$ ; June, Mann-Whitney  $W = 439.5$ ,  $P < 0.001$ ), with a higher median sole egg abundance associated with sediment containing  $< 30\%$  gravel (Table 3). Median and 95<sup>th</sup> percentiles of egg abundance for the two final sediment classes within each month were used as input to the habitat models, with the 95<sup>th</sup> percentile used as an estimate of the upper limit of sole egg abundance within each sediment class.

Figure 4 shows the digital map developed for depth, and examples of those developed for temperature and salinity. To minimise interpolation error, the temperature and salinity digital maps were not extrapolated to the north and east beyond a distance equivalent to that separating the survey points at the edge of the survey area. In addition, to ensure spatial coherency the raster maps were not extended to the south and west beyond the area covered by the depth map. For all months the coastal regions were generally characterised by lower salinities, and with the exception of March, warmer temperatures. In March a tongue of warmer water was situated offshore in the eastern English Channel, and was approximately 1 – 1.5 °C warmer than the coastal waters.

The monthly prediction models are shown in Figure 5, with those based on upper estimates predicting a higher abundance of sole eggs for spatially-coincident cells compared to the models based on central estimates. The central and upper models depicting relative spawning habitat suitability for the entire spawning season are shown in Figure 6. In all cases the areas of highest suitability are located near to the coastline and in association with offshore sandbanks, with lowest suitability scores found within the deeper water areas and in association with the sediments

containing > 30% gravel. Both final models predicted a similar proportion of habitat in each of the four classes (Table 4).

In order to quantitatively evaluate the predictive power of the final habitat models, the test data were first associated with the predicted suitability scores from both central and upper models. The test dataset was then partitioned into four classes based on quartiles of the suitability scores. Both the central and upper model were successful in predicted a higher mean sole egg abundance with increasing habitat suitability class (Table 5), with significant differences ( $P < 0.05$ ) found between the first and third, and first and fourth quartile classes.

## Discussion

Depth, temperature, salinity and sediment type were all found to be related to the distribution of stage 1a sole eggs during at least one month in the March to June 1991 spawning season. Temperature was positively related during March only, with low egg densities found in temperatures below 7 °C. Along the east coast of England, Riley (1974) found sole eggs in low densities in water temperatures below 10 °C. Similar findings are reported by Koutsikopoulos and Lacroix (1992) for the Bay of Biscay where the majority of eggs collected were found at temperatures above 9 °C. The results of this study also suggests that sole spawn when temperatures rise above a certain minimum. However it remains unclear whether a rise in temperature during the early spring acts to trigger spawning, or whether spawning cannot be detected in waters of low temperature due to high natural mortality of sole eggs. In contrast to March, the regression quantile models developed for May and June suggests a slight decrease in abundance of sole eggs with increasing temperature. The range of temperatures encountered during these two months (8.8 – 13.3 °C) would not be expected to elicit any major differences in spawning activity. The response seen may therefore represent slight differences in the timing and period of spawning activity resulting from the spatial differences in the temperature encountered during the entire spawning period.

A negative relationship between egg abundance and depth was found for all four months, confirming the preference displayed by the sole to spawn in the shallow water regions of the eastern English Channel and southern North Sea (Borremans, 1987; Van der Land, 1991; ICES, 1992). Larval transfer to the inshore nursery grounds would be facilitated by this behavioural mechanism. However, local hydrodynamics are also thought to contribute towards larval transport and spawning success, particularly where sole stocks are found to inhabit regions characterised by deeper waters, such as the Bay of Biscay (Koutsikopoulos and Lacroix, 1992), and the Bristol Channel (Horwood, 1993; Symonds and Rogers, 1995). Similar mechanisms may also be in place in the eastern English Channel (Grioche, 1998).

A relationship between egg abundance and salinity is suggested during April and May, although the responses predicted in each month are in direct contrast. The strong negative relationship between salinity and egg abundance in May suggests a preference exists for the lower salinity water found along both the English and French inshore regions, whilst a weaker, positive relationship suggests the converse is true in April. In May the salinity over the whole region is generally lower, particularly along the eastern English coast where the difference in salinity is between 0.3-0.9 psu. The drop in salinity during this month may have elicited a clearer response pattern, one of adult sole spawning predominantly within the more inshore and less saline waters. However, as depth, proximity to riverine outflows, and distance to the shore could all be considered inter-correlated with salinity, it is difficult to untangle the actual environmental cues the sole might be responding to, particularly as they are capable of tolerating a much wider salinity range than that encountered

within the spatial limits of the survey (Marchand, 1991). Consequently salinity would not be acting as a limiting factor to spawning activity as suggested by the model, but may instead represent the best predictor to describe the distribution of sole eggs in May.

A clear relationship was found between egg abundance and sediment type with consistently higher densities found over sediment with a < 30% gravel content. The preference for sandy and finer-grained sediments by both juvenile and adult sole is well documented (Rogers, 1992; Koutsikopoulos and Lacroix, 1992; Horwood, 1993; Kaiser *et al.*, 1999). Sole bury themselves into sandy substratum during the day and feed during the night on a variety of infaunal invertebrates associated with finer-grained sediments (Lagardère, 1987). Whilst sandy sediments cover most of the eastern English Channel and southern North Sea, the distribution of sole eggs and therefore of spawning adults is far from uniform. Habitat definition can only be defined at the spatial resolution of the underlying data, and clearly the broad categorisation will in reality consist of a gradation of sediment types, interspersed by patches of varying structural complexity, which are difficult to resolve either spatially or temporally. Within this heterogeneity, sole may also only occupy a limited range of the habitat variable dependent on the population size, with a wider range occupied with increasing population density (Gibson, 1994). Consequently, both heterogeneity of habitat types, and variability of habitat use will all contribute substantially towards the variability inherent to plots of species-habitat relationships (Rogers, 1992). By modelling the upper limits of the abundance of sole eggs within both the broad categories of sediment type and the continuous variables of temperature, salinity and depth, we can ensure that the relative suitability of the habitat factor is not underestimated, or at least underestimated to a lesser degree than estimates of central tendency.

As expected, the upper quantile models developed for each month predicting a higher abundance of sole eggs in comparison to those based on central estimates. Both central and upper habitat suitability models performed equally well when evaluated with an independent dataset and generally depicted similar habitat suitability scores at each spatial location. Whilst these final maps may not hold any particular meaning for any one month, they do provide a collective view of spawning habitat suitability for the region and indicate where spawning activity might be at its greatest during the spawning season.

Clearly the benefits of using regression quantiles lie in their ability to provide better quantitative estimates of the upper limits to the species response (in this case spawning activity) imposed by the measured habitat factors. In doing so, regression quantiles are able to detect the effect of limiting factors in some upper quantiles that may not be directly evident in models based on central estimates. An example is during April where the 50<sup>th</sup> quantile could not be estimated, whereas both depth and salinity were found to be significant at the 75<sup>th</sup> quantile. The lack of a detectable relationship at the 50<sup>th</sup> quantile in April reminds us that although the central habitat suitability model performed equally well, it was based on three, instead of four monthly prediction models, and therefore cannot be considered to be as reliable as the model based on upper estimates.

The models of spawning habitat suitability for the sole developed in this study are far from definitive, but represent a methodology to achieve more realistic definitions and maps of fish habitat when only a limited number of habitat variables are available. Whilst this has a tendency to oversimplify a complex system (Rogers, 1992), the use of a few, simple to measure abiotic habitat predictors is justified if the statistical modelling technique can potentially account for unmeasured habitat factors by providing estimates at the upper bounds of the biological response. In addition, it must be recognised that the complexity of an ecological system is in part defined by the inter-correlation of both abiotic and biotic factors, and therefore habitat models that attempt to



incorporate increasing numbers of factors may not necessarily achieve greater predictive power. It has also been argued that functional relationships based on central estimates of the biological response contradict the ecological theory of limiting factors (Thomson *et al.*, 1996). Therefore techniques limited to relying on such estimates do little to progress our understanding of biological responses to those environmental variables that determine habitat spatial location and suitability. By providing estimates at the upper limits of species-habitat distributions, changes expected when the measured variable is the active limiting factor can be estimated. Models based on upper limits therefore represent conservative estimates of habitat suitability, which may be more desirable from a fisheries conservation perspective.

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Table 1. Mean (and SE) number of stage 1a sole eggs during March to June 1991, and associated physical parameters. The location of survey points is shown in Figure 1.

	<i>n</i>	No. of eggs m <sup>-2</sup>	Water column temperature (°C)	Water column salinity (psu)	Chart depth (m)
March	67	1.6 (0.36)	7.69 (0.064)	34.97 (0.068)	29.9 (1.69)
April	69	4.7 (1.22)	8.85 (0.041)	35.03 (0.060)	30.0 (1.63)
May	83	2.2 (0.39)	9.91 (0.057)	34.81 (0.057)	29.8 (1.41)
June	71	0.6 (0.16)	11.31 (0.077)	34.85 (0.062)	30.1 (1.67)

Note: salinity mean and standard error for June based on 67 points due to missing data.

Table 2. Regression quantile parameter estimates and associated significance for changes in stage 1a sole egg abundance expressed as no. m<sup>-2</sup> (log<sub>e</sub> [y + 1] transformed) according to temperature (°C), salinity (psu), and depth (m) in 1991. T\*D is temperature-depth interaction and T\*S is temperature-salinity interaction. Significance of the whole model is also given where appropriate.

	Quantile	Constant	Temp	Depth	Salinity	T*D	T*S	Whole model
March	94	-5.225	1.020*	-0.0004*		-0.004*		*
	50	-4.962	0.789**	0.084*		-0.014*		**
April	79	-33.816		-0.046*	1.051*			*
May	88	-76.980	10.550**		2.386***		-0.316*	***
	50	8.367	-0.685*	-0.030**				**
June	87	2.406	-0.069*	0.099**		-0.012**		**
	50	0.373		-0.007**				

NB: \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$

Table 3. Monthly median and 95<sup>th</sup> percentile abundance of sole eggs (no. m<sup>-2</sup>) according to sediment type.

	Sediment Type	<i>n</i>	Median	95 <sup>th</sup>
March	> 30% gravel	25	0.09	2.19
	< 30% gravel	19	1.85	11.46
April	> 30% gravel	27	0.29	3.74
	< 30% gravel	18	7.58	39.55
May	> 30% gravel	28	0	6.20
	< 30% gravel	26	1.98	9.28
June	> 30% gravel	25	0	0.89
	< 30% gravel	21	0.83	2.31

Table 4. Summary table showing the area (in km<sup>2</sup>) encompassed by each habitat suitability (HS) class for both central and upper models of spawning habitat suitability for the sole.

HS class	Upper model		Central model	
	Area	%	Area	%
0.75 – 1.00	440.5	2.8	571.8	3.4
0.50 – 0.75	4461.6	28.3	5261.1	31.1
0.25 – 0.50	5390.9	34.2	3884.3	23.0
> 0 – 0.25	5485.6	34.7	7202.4	42.5

Table 5. Mean habitat suitability (HS) and mean sole egg abundance with associated 95% confidence intervals for both upper and central habitat suitability models. Mean number of sole eggs within each model with a letter in common indicates a significant difference ( $P < 0.05$ ).

	<i>n</i>	HS	No. eggs m <sup>-2</sup>	95% CI	
Upper model	10	0.22	8.5	4.68 – 15.55	xy
	9	0.35	15.5	6.70 – 36.07	
	10	0.48	36.3	19.53 – 67.60	x
	10	0.56	38.6	17.01 – 87.61	y
Central model	10	0.03	8.5	4.68 – 15.55	xy
	9	0.26	16.0	6.74 – 37.93	
	10	0.53	35.4	19.13 – 65.61	x
	10	0.61	38.6	17.01 – 87.61	y

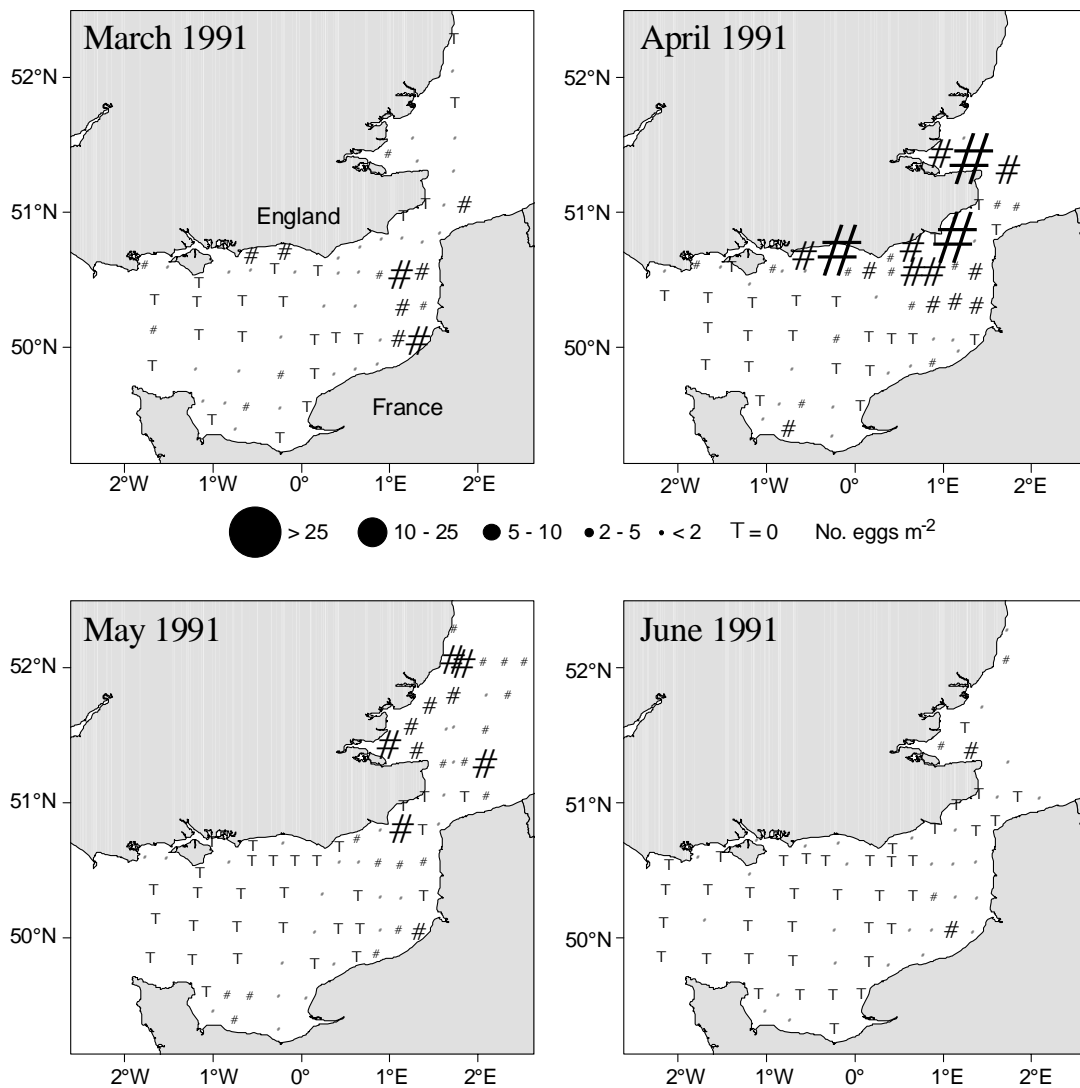


Figure 1. Distribution of stage 1a sole eggs in the eastern English Channel and southern North Sea from March to June 1991. England coastal boundary data, ©Crown and Ed-LINE.

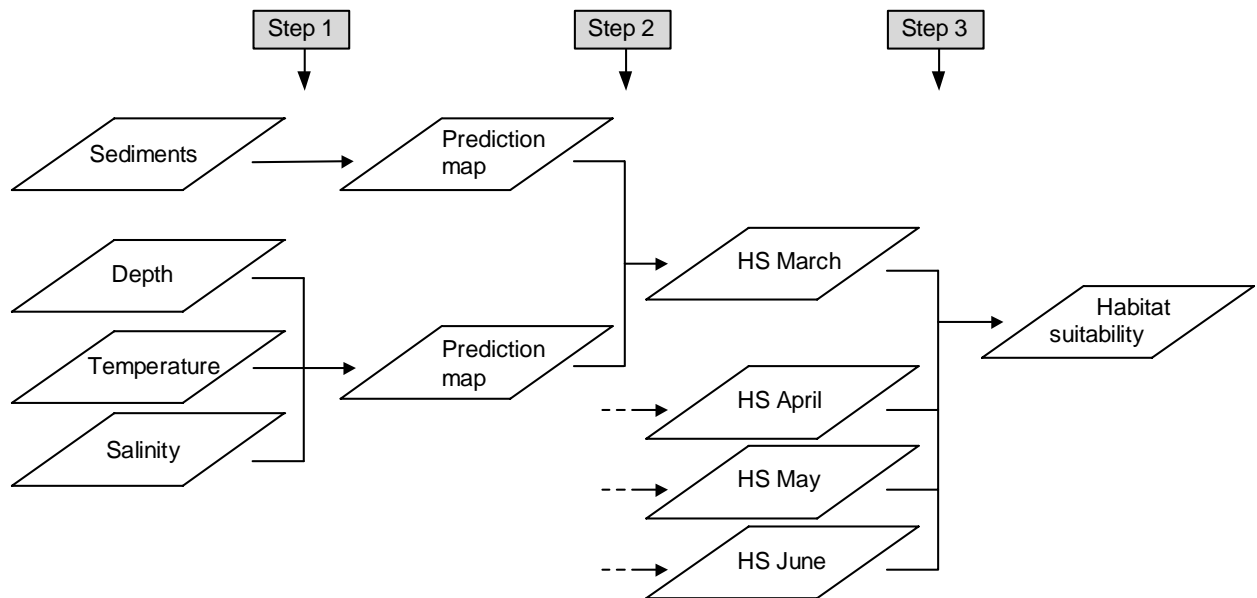


Figure 2. Diagrammatic representation of the modelling procedure. **Step 1**; depth, temperature and salinity digital maps are re-coded using the regression quantile coefficients, and the sediment map is re-coded with the abundance percentiles for each sediment class. **Step 2**; the geometric mean is calculated for each spatially-coincident grid cell in the two prediction maps to produce monthly habitat suitability (HS) maps. **Step 3**; the maps are converted to a relative scale (0-1) and the arithmetic mean of each spatially-coincident cell in the monthly HS maps is calculated to produce an overall habitat suitability map.

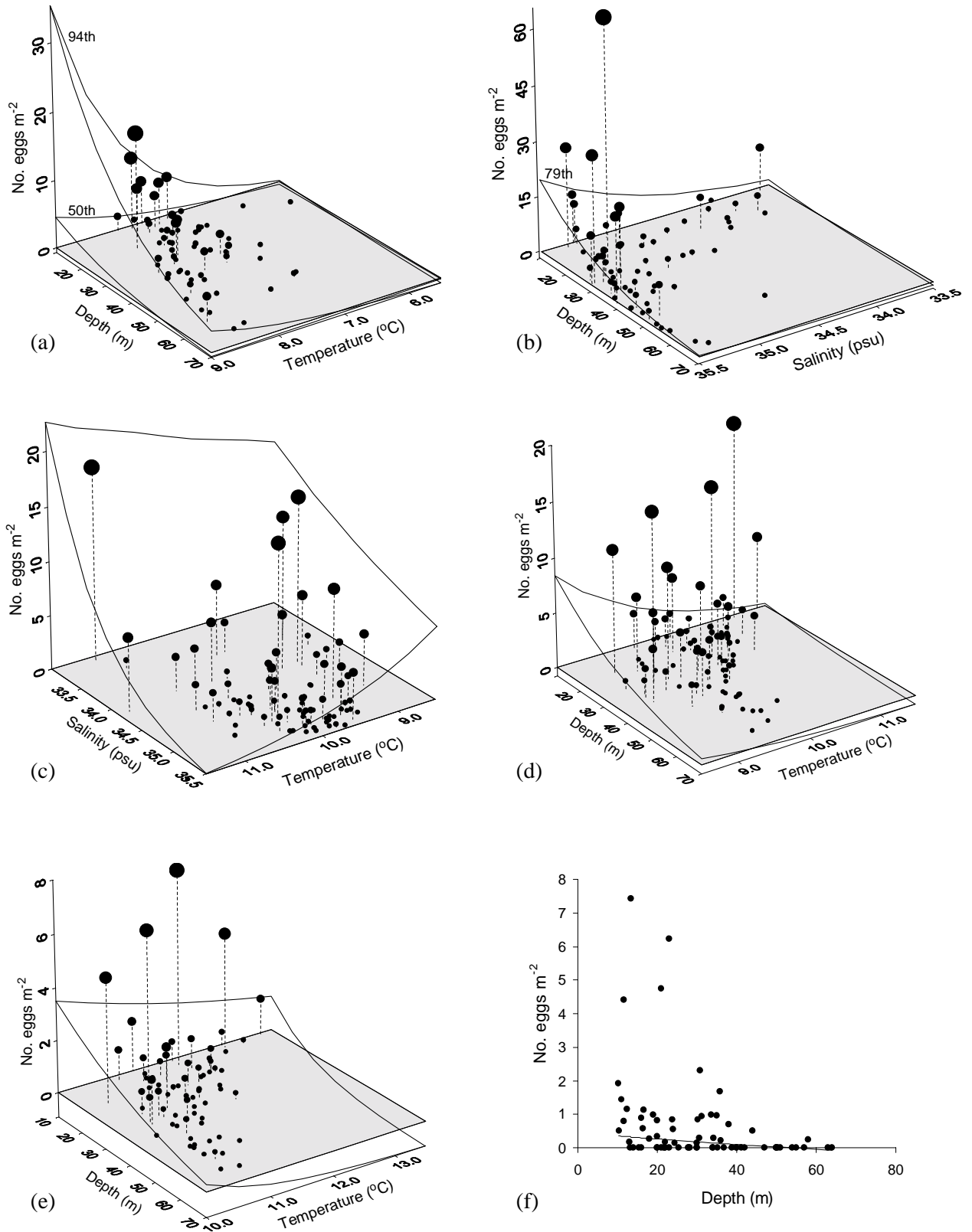


Figure 3. Abundance of stage 1a sole eggs and associated regression quantile models based on parameter estimates given in Table 2 for, (a) March 50<sup>th</sup> and 94<sup>th</sup>, (b) April 79<sup>th</sup>, (c) May 88<sup>th</sup>, (d) May 50<sup>th</sup>, (e) June 87<sup>th</sup>, and (f) June 50<sup>th</sup>. Zero egg abundance is depicted by the shaded plane.

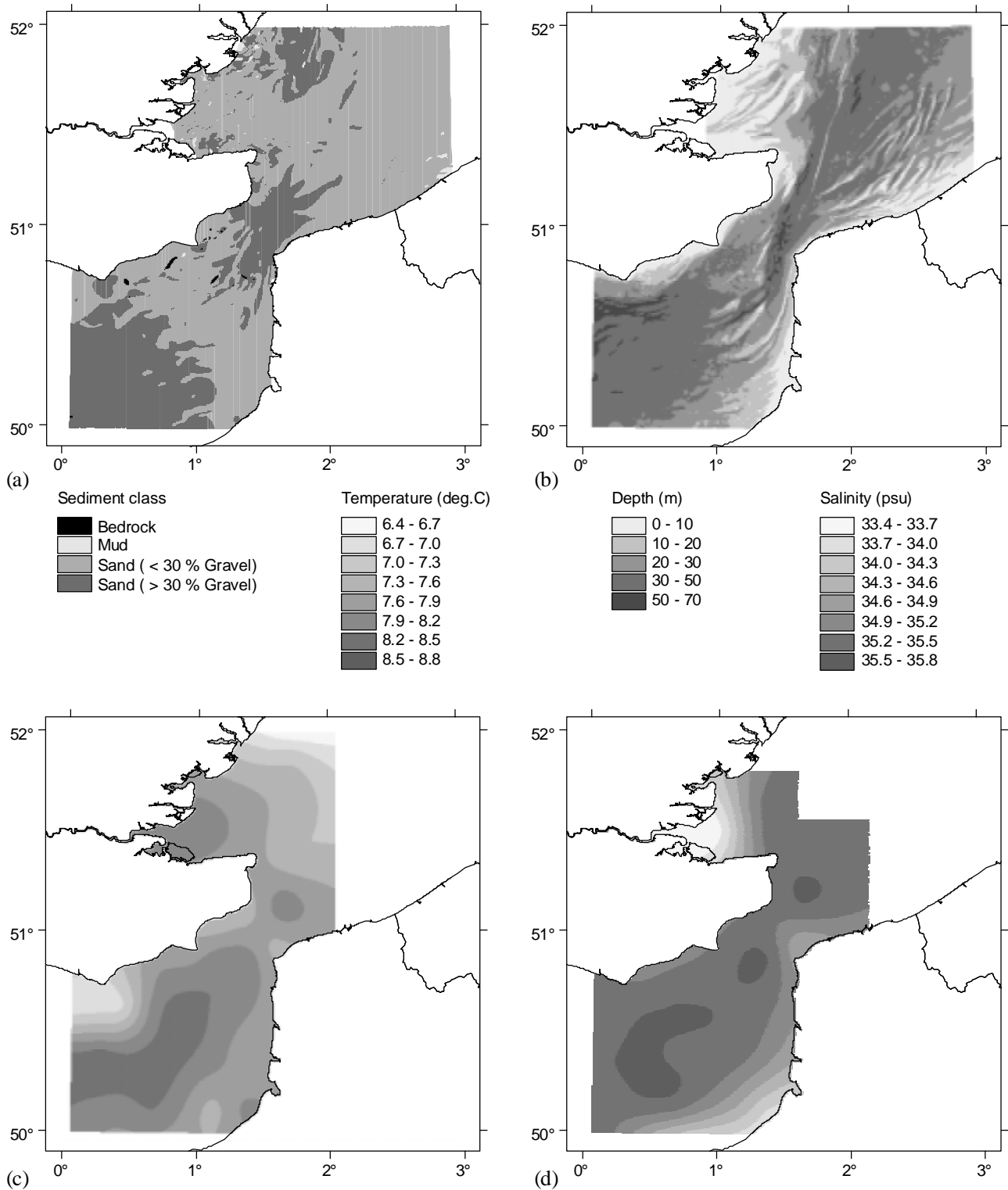


Figure 4. Examples of the environmental maps for the eastern English Channel and southern North Sea used to develop the habitat models: (a) sediment type, (b) depth, (c) mean water column temperature in March, (d) mean water column salinity in April. Depth digital map reproduced from Admiralty Chart nos. 1406, 1607, 1975, 2449, 2451 and 2656 by permission of The Controller of Her Majesty's Stationery Office, the Port of London Authority, and the hydrographic offices of Belgium, France, The Netherlands and the United Kingdom. Sea-bed sediments digital map reproduced from British Geological Survey UTM map sheets (Dungeness to Boulogne, Thames, and Ostend) at the original scale of 1:250 000. Licence 99/80, British Geological Survey. ©NERC. All rights reserved. England coastal boundary data, ©Crown and Ed-LINE.



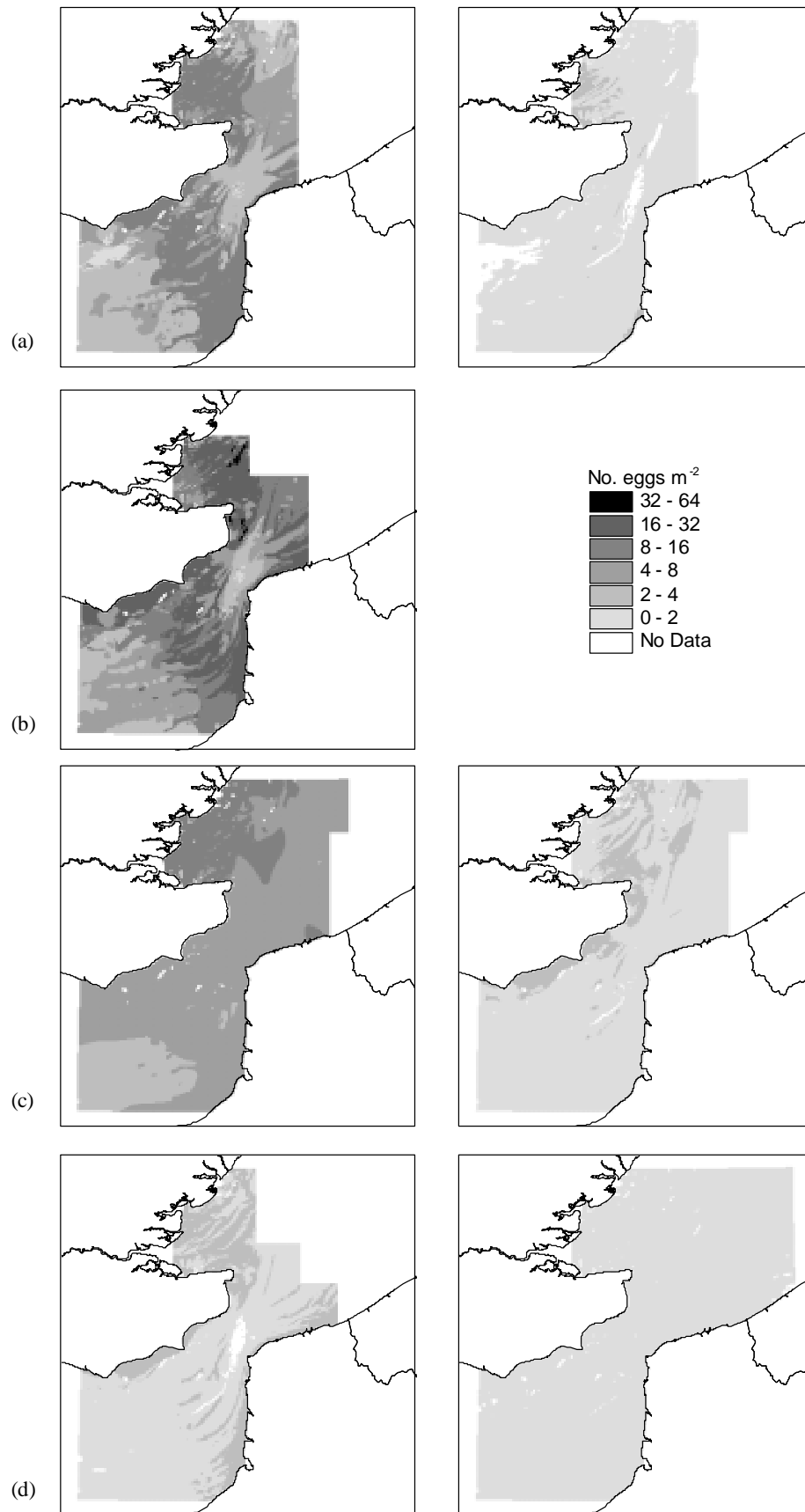


Figure 5. Predicted abundance of sole eggs developed from both upper (left) and central (right) estimates in (a) March, (b) April, (c) May and, (d) June 1991 for the eastern English Channel and southern North Sea. England coastal boundary data, ©Crown and Ed-LINE.

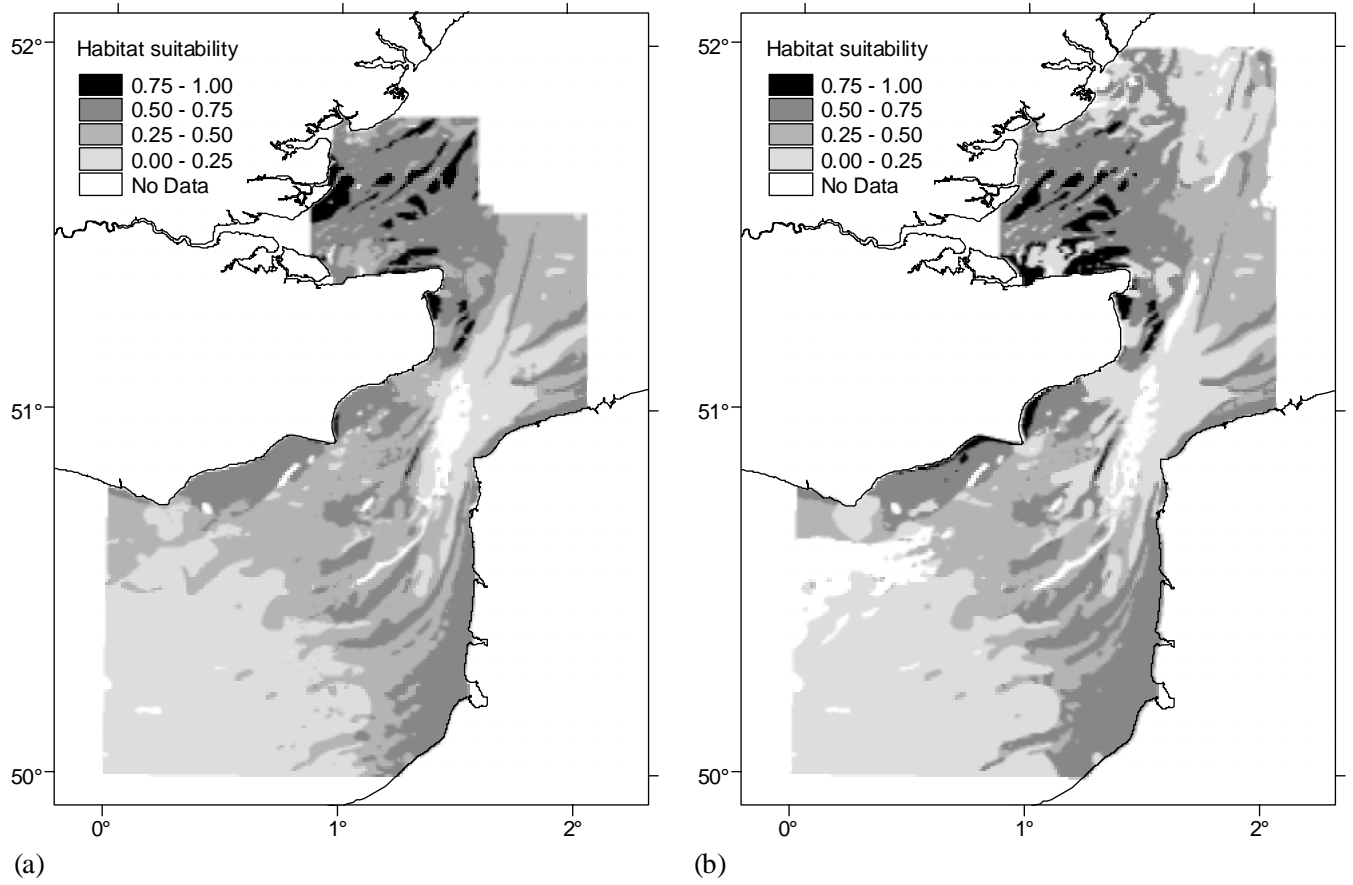


Figure 6. Spawning habitat suitability models for the sole in the eastern English Channel and southern North Sea. (a) Model based on upper estimates, and (b) model based on central estimates. England coastal boundary data, ©Crown and Ed-LINE.