What influences European plaice (*Pleuronectes platessa*) distribution in the eastern English Channel? Using habitat modelling and GIS to predict habitat utilization

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Conservation of fish habitat requires knowledge of how spatial distributions of species are related to environmental factors. Habitat modelling and mapping are useful in predicting species–environment relationships. Species abundance is modelled as a function of environmental parameters to understand species habitat utilization better. The influence of environmental factors on plaice (*Pleuronectes platessa*) distribution was investigated for two life stages and over two seasons. Generalized linear modelling and quantile regression modelling were used to relate the relative abundance of (juvenile and adult) fish to environmental predictors (seawater temperature, salinity, water column depth, bed-shear stress, and sediment type) in autumn and summer. The resulting regression parameters were used to map preferential and potential habitat distributions within a geographic information system. Models were evaluated by comparing predicted against observed abundances. Seabed sediment type was the main significant predictor of plaice preferential and potential habitats, whereas other factors did not show such a clear influence. The results contribute to a better understanding of the spatial ecology of the species.

Keywords: distribution, fisheries, flatfish, GLM, QR.

Introduction

Ecosystem-based management approaches appear to be the most efficient way to achieve the goal of sustainable fisheries (Link, 2002). A necessary component of this approach is the identification and understanding of habitat utilization, including how the environment can influence species distribution patterns on various spatial and temporal scales and during different life stages (McConnaughey and Smith, 2000; Martin *et al.*, 2009). For this purpose, it is important to consider the relationships between species and habitat, where habitat is defined as the set of environmental factors defining the conditions of presence, survival, growth, and reproduction of a given species.

In natural systems, changes in environmental factors influence the distribution of species and their use of habitat. If conditions change markedly, species will attempt to maintain themselves in locations that are as favourable to growth and survival as possible (Gibson, 1997). The requirements of individual fish do not remain constant during their development, so a suitable habitat for larvae may not be suitable for juveniles or adults (Martin *et al.*, 2010). The transition from one life-history phase to the next is often accompanied by a change in habitat preference. For example, young age classes are particularly vulnerable to predators and extremes of environmental conditions and are often concentrated in nursery areas where the trade-off between growth and survival is optimized (Gibson *et al.*, 2002).

A topical research theme in fishery ecology is the relationship between species and their environment. Habitat modelling (modelling species distribution) and geographic information systems (GIS) are important and innovative tools utilized to try to understand better how species make use of their habitat (Guisan and Zimmerman, 2000; Eastwood *et al.*, 2003). One of the most used techniques to model species distribution is generalized linear modelling (GLM), but also GAMs, in which the mean (central tendency) species response to environmental factors is estimated (Oksanen and Minchin, 2002). GLMs describe and predict the preferential habitat (the portion of potential habitat used on average over time), but do not properly estimate the limiting effect of the environment on species distribution (Cade *et al.*, 1999). As the growth rate of a species is determined by the most limiting resource (Hiddink and Kaiser, 2005), the real response of a species to a given limiting factor can only be quantified if all other factors are at non-limiting levels, which is unlikely in nature. The meaningful determination of the limiting effect of environmental variables on species response requires a study of the upper bounds of species abundance response to environmental factors. The use of quantile regression (QR), whereby any relative limit (quantile) of the observed data distribution may be modelled rather than the mean (Cade and Noon, 2003; Koenker, 2005),

allows estimation of the effects of limiting factors on species abundance and the description of potential (or maximal) habitat (Vaz *et al.*, 2008).

GLM and linear QR were used for modelling the habitat use of European plaice (*Pleuronectes platessa*) in the eastern English Channel, an important area for marine resources and fisheries (Carpentier *et al.*, 2005). European plaice are bentho-demersal fish that around the British Isles spawn and recruit mainly (75–80%) in the English Channel (Nash *et al.*, 2000). They are exploited by several countries (France, Belgium, and the UK) and represent the most abundant benthic fish species landed from the eastern Channel (Mahé *et al.*, 2006). However, in the past 20 years, plaice landings have more than halved (from 8366 t in 1978 to 3146 t in 2006; ICES, 2008).

In this context, it is necessary to improve our knowledge of the spatial distribution of the species at various life stages to provide information for effective management. Previous studies have tried to relate the distribution of flatfish to single environmental factors, e.g. depth, temperature, and sediment type (Smale *et al.*, 1993; Albert *et al.*, 1998; Ellis *et al.*, 2000; Amezcua and Nash, 2001), but the general knowledge of how these species use and change their habitat during different life stages using a complex approach (testing several environmental predictors together) remains poor. Younger fish, because of their smaller body size, may be more limited in their swimming and competitive abilities and may be confined to smaller or different areas from older, bigger fish. Moreover, the environment of the eastern English Channel is subject to seasonal variation (Carpentier *et al.*, 2009), notably in terms of temperature and salinity spatial patterns. Models were therefore developed for two seasons (summer and autumn) and two life stages to study possible seasonal and onto-genetic changes in habitat utilization.

Material and methods
Survey data
The Centre for Environment, Fisheries and Aquaculture Science (Cefas) conducted a Beam Trawl Survey (BTS) annually in July/August between 1989 and 2006. Samples were collected using a commercial 4-m beam trawl at fixed stations, following a depth-stratified sampling strategy. The standard annual survey had a total of ~100 stations (Figure 1a). The gear had a minimum mesh size of 40 mm and was towed at 4 knots (ground speed) for 30 min at a warp length adjusted to bottom depth. Water column depth, temperature, and salinity were recorded using sensors attached to the beam trawl; temperature/salinity data were not available for all stations and years.

The Channel Ground Fish Survey (CGFS), a survey by the Institut Français de Recherche pour l'Exploration de la Mer (Ifremer), was carried out each year in October between 1988 and 2006 on board the research vessel "Gwen Drez". The survey extended from the eastern English Channel to the southern North Sea (Figure 1b). The study area was subdivided into rectangles of 15′ latitude and 15′ longitude using a systematic sampling strategy. The sampling gear was a very high (3 m) vertical opening bottom trawl (also known as a GOV trawl) with a minimum 10-mm mesh in the codend. Trawls lasted 30 min at an average speed of 3.5 knots. This sampling gear is well adapted to the various seabed types encountered in the study area. Between 1997 and 2006, temperature and salinity (surface and
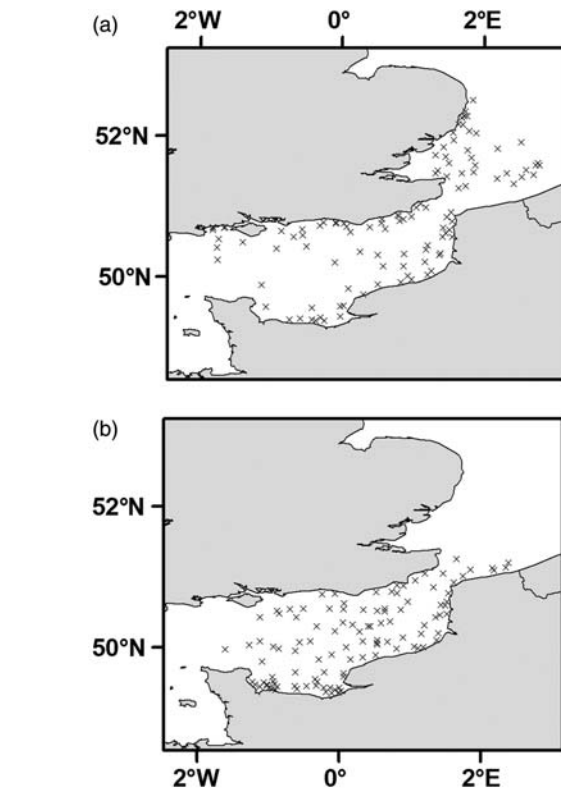
Figure 1. Stations sampled in 2006 during (a) the BTS, and (b) the CGFS surveys (fixed station sampling schemes).

bottom) were also measured, using a sensor attached to the headline of the trawl.

For both surveys, the fishing method was standardized: sampling stations each year were at similar locations, and identical sampling gear was used. After each haul, all fish were sorted, identified, counted, and their length measured.

Abundance indices at each station were standardized to density (number of fish per km^2), which was tested for normality (using histograms, skewness, and kurtosis) and log-transformed [$\log_{10}(x + 1)$, where x is density, to reduce the skewness of the distribution (Legendre and Legendre, 1998)]. Such a transformation is widespread in numerical ecology (Legendre and Legendre, 1998) and has a fairly similar effect on the data to a direct $\log(x)$ transformation when data values are >0.1, as is the case here. Length at age 1 was estimated using the von Bertalanffy growth function (von Bertalanffy, 1938), then used to separate data for 0-group (<18.0 cm) and 1+ group (≥ 18.1 cm) fish. Both surveys were designed to target different components of the fish fauna and did not catch all species with equal efficiency. Nevertheless, for plaice, both life stages were well represented in the catches (Figure 2).

Environmental predictors
For habitat modelling, sea surface temperature and salinity, water column depth (all three measured during the surveys described above), bed-shear stress, and seabed sediment type (Larsonneur *et al.*, 1979) were used as predictors (see a summary of the observations in Supplementary Table S1). Five main categories of seabed deposit were used: pebble, gravel, coarse sand, fine sand,
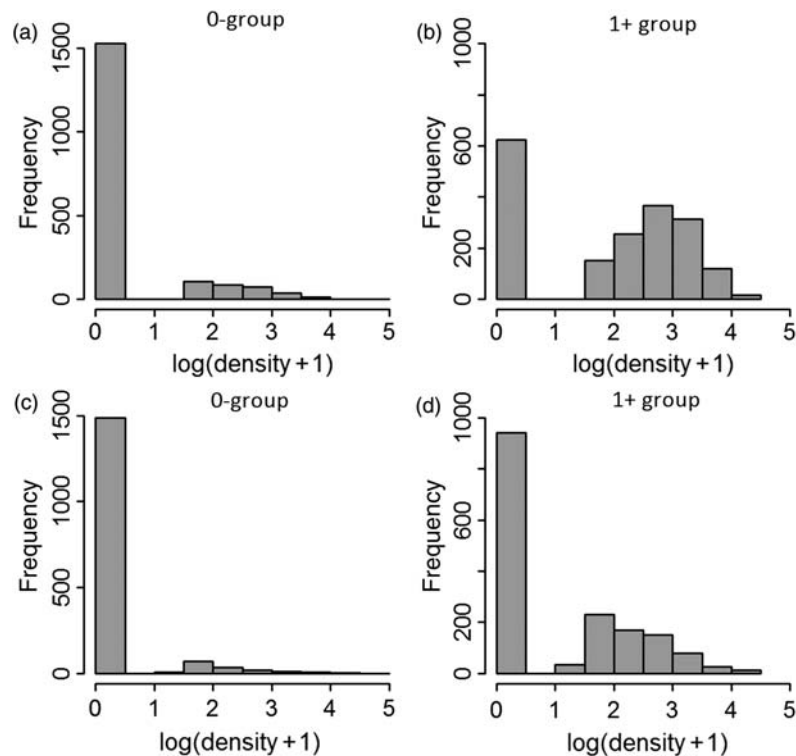
Figure 2. Frequency of plaice densities (log-transformed) for (a) 0-group plaice in the BTS, (b) 1+ year plaice in the BTS, (c) 0-group plaice in the CGFS, and (d) 1+ year plaice in the CGFS.

and mud. Bed-shear stress (in Newton m^{-2}) was estimated using a two-dimensional hydrodynamic model of the northwest European shelf developed at the Proudman Oceanographic Laboratory (Aldridge and Davies, 1993). It was used as a proxy for bed friction resulting from tidal currents. Preliminary studies of single variable relationships between species density and environmental predictors showed that these were close to linear, as expected because the range of environmental variables was relatively narrow. As a result, GLMs and linear QRs were preferred to GAMs and non-linear QRs. However, second-order polynomials were added as continuous variables to increase model flexibility in depicting the species response. Correlations among explanatory variables were tested before model development. Preliminary exploratory analyses showed that none of them were truly co-linear, so all environmental variables were tested including first-order interactions.

Habitat modelling
The strong discontinuity between the zero values and positive density data (Figure 2) leads to a two-stage approach, where (i) presence/absence and (ii) density models were selected separately, and a delta model evaluated. In the particular case of trawl samples, as a consequence of both trawl geometry and species behaviour, zero observations may indicate either low density or true absence, with different processes governing presence probability and density levels (Martin *et al.*, 2005). A two-step approach therefore seemed suitable (Stefánsson, 1996; Barry and Welsh, 2002), first modelling the presence/absence data using a binomial distribution and logit link function, then modelling presence-only data (i.e. positive log-transformed densities) using a Gaussian distribution with a canonical (i.e. identity) link function. Model

selection was carried out through backward selection based on Chi-squared tests (presence/absence data) or *F*-tests (presence-only data) at a test level of 0.05. This approach was chosen rather than the Akaike information criterion to be coherent with the QR selection procedure that uses significance tests for variable selection. The binomial model predicted the probability of presence (or probable habitat), and the Gaussian model predicted positive density levels on a log scale. The probability of presence was then multiplied by the predicted density level to obtain the final predicted value or preferential habitat model (also referred to as a delta model).

Linear QRs were estimated for five quantile intervals ranging from the 75th to the 95th using the variable selection procedure proposed by Vaz *et al.* (2008), based on backward elimination. Significance tests of all second-order polynomials and interactions were made, and the variable associated with the largest *p*-value across the five quantiles was removed from the model (when >0.05). The reduced model was re-run for all five quantiles and significance tests performed again to eliminate additional variables according to the same rule, until all remaining variables were significant for at least one quantile. Main effects were tested only when associated interactions and the second-order polynomials had been eliminated. If the resulting model had all variables significant over more than one quantile, the highest of these quantiles was selected as the model best representing the upper bounds of species catch density limited by the environmental variables. The coefficients of the final models were then used, within a GIS, to produce habitat maps.

For each habitat model, the adjusted coefficient of determination (also known as adjusted R^2) was used to measure the goodness of fit. The adjusted coefficient of determination

accounts for the number of observations and explanatory parameters (Legendre and Legendre, 1998).

All modelling was carried out using the R software and its MASS (version 7.3-5) package.

Model evaluation and uncertainty

For evaluating all final fitted delta GLMs and QRs, observed and predicted values were compared using Spearman's rank correlation coefficient (r_s) and its associated p-value, because r_s does not assume a linear relationship. In addition, a Wilcoxon signed-rank test was applied to pairs of observations and mean predictions. This test was preferred to others because it does not require any distributional assumptions. For a Spearman's rank correlation test, the test was considered passed if $p < 0.05$ and $r_s > 0.1$. For the Wilcoxon signed-rank test, the null hypothesis of the test is that observed and predicted values are unrelated, so it was considered passed if $p > 0.05$.

For QR models, a correct classification (CC) test, defined by the proportion of observed values in the evaluation dataset that fall below those predicted (Eastwood *et al.*, 2003) was used. To increase the robustness of this test, the results of which may be strongly affected by data heterogeneity, a resampling procedure was adopted. For each model, 1000 resampled datasets were produced by resampling with replacement separately the initial dataset of observed and predicted values. The test was considered passed if the selected quantile for a particular model was less than the upper confidence limit of the bootstrapped proportion of CC.

As the evaluation tests were relatively permissive, the relative prediction or model error (defined as the absolute difference between observed and predicted species abundance and/or probability of presence relative to the maximum observed value) and the pattern of residuals as a function of the original observation were also explored to check model fit. For QRs, however, the error was set to zero if the observed value was lower than the predicted value (which is the expected behaviour of that type of model). The spatial distribution of the model error ratios was mapped for each model, a value of 1 corresponding to the maximum possible prediction error. The model prediction error can therefore be interpreted as a percentile of model uncertainty.

To interpret regression coefficients in the presence of interactions and polynomial terms, presence probabilities and densities were predicted for the observed range of values of the significant explanatory variables to illustrate the species response along one given environmental gradient, all other variables remaining constant at their mean value (Elith *et al.*, 2005; Vaz *et al.*, 2008). In addition, survey density distribution maps were created in ArcGIS (ESRI, ArcGIS 9.1) to be compared with mapped model predictions.

Mapping model predictions

For each life stage (0-group or 1+ group) and season (summer or autumn), GLM and QR models were developed using depth, temperature, and salinity measured *in situ* at each station during the surveys. For bed-shear stress and seabed sediment type, the information was extracted (using a GIS) at each survey location from digital continuous maps of these parameters, then used for model development. For mapping model predictions, these two maps (of bed-shear stress and seabed sediment type) were used directly. For depth, a continuous digital map was produced that merged bathymetry and mean sea level (corresponding to a mid-tide coefficient) derived from a three-dimensional hydrodynamic model (Le Roy and Simon, 2003; see Carpentier *et al.*, 2009, for further detail). The temperature and salinity digital maps were produced by averaging annually interpolated survey maps for the period 1988–2006 (Carpentier *et al.*, 2009). The fitted final models together with local environmental variables were then used to produce predicted values on a fine grid; these were then mapped within the GIS.

Results
Environmental factors relevant to plaice habitat

In all, 12 models were developed to cover the probable/preferential (GLM) and potential (QR) habitats of 0-group and 1+ group

Table 1. Significant predictors of the GLM and RQ models, along with the number of significant interactions and the proportion of variance explained by the models.

| Period	Life stage	Model	Salinity	Depth	Temperature	Bed-shear stress	Sediment	Interaction	Adjusted R^2
GLM									
July/ August	0-group	Presence	+	−	+	bell	M-CS-FS-P-G	stress:sed and sal:depth	0.29
		Density	+	−	+	+		stress:sal, stress:depth, and sal:depth	0.13
	1+	Presence		+/−		−	G-M-CS-FS-P	temp:sed and depth:sed	0.30
		Density	−2	−	−	+	M-P-G-FS-CS	stress:sed, sal:temp, sal:depth, and temp:sed	0.16
October	0-group	Presence	+	+2		−2	M-FS-CS-G-P	stress:depth and depth:sed	0.43
		Density		−	−2				0.17
	1+	Presence		+2	+2	+	FS-M-G-CS-P	stress:sal and depth:sed	0.39
		Density		−	+				0.13
Regression quantiles									
Jul/Aug	0-group	RQ 95		−	+	−	M-P-FS-CS-G	depth:sed and stress:sed	0.19
	1+	RQ 95			+	+	P-G-M-FS-CS	stress:sed	0.16
October	0-group	RQ 95					M-FS-G-CS-P	depth:sed	0.81
	1+	RQ 90	−	−	+	+	G-CS-FS-P-M	stress:sed, sal:sed, and temp:sed	0.33

−/+ indicates that the variable was significant at the α level of 0.05 and that the regression coefficient was negative/positive, and bell that the second-order polynomial term was significant. Seabed sediment types are listed in the order of decreasing regression coefficients (M, mud; FS, fine sand; CS, coarse sand; G, gravel; P, pebble).
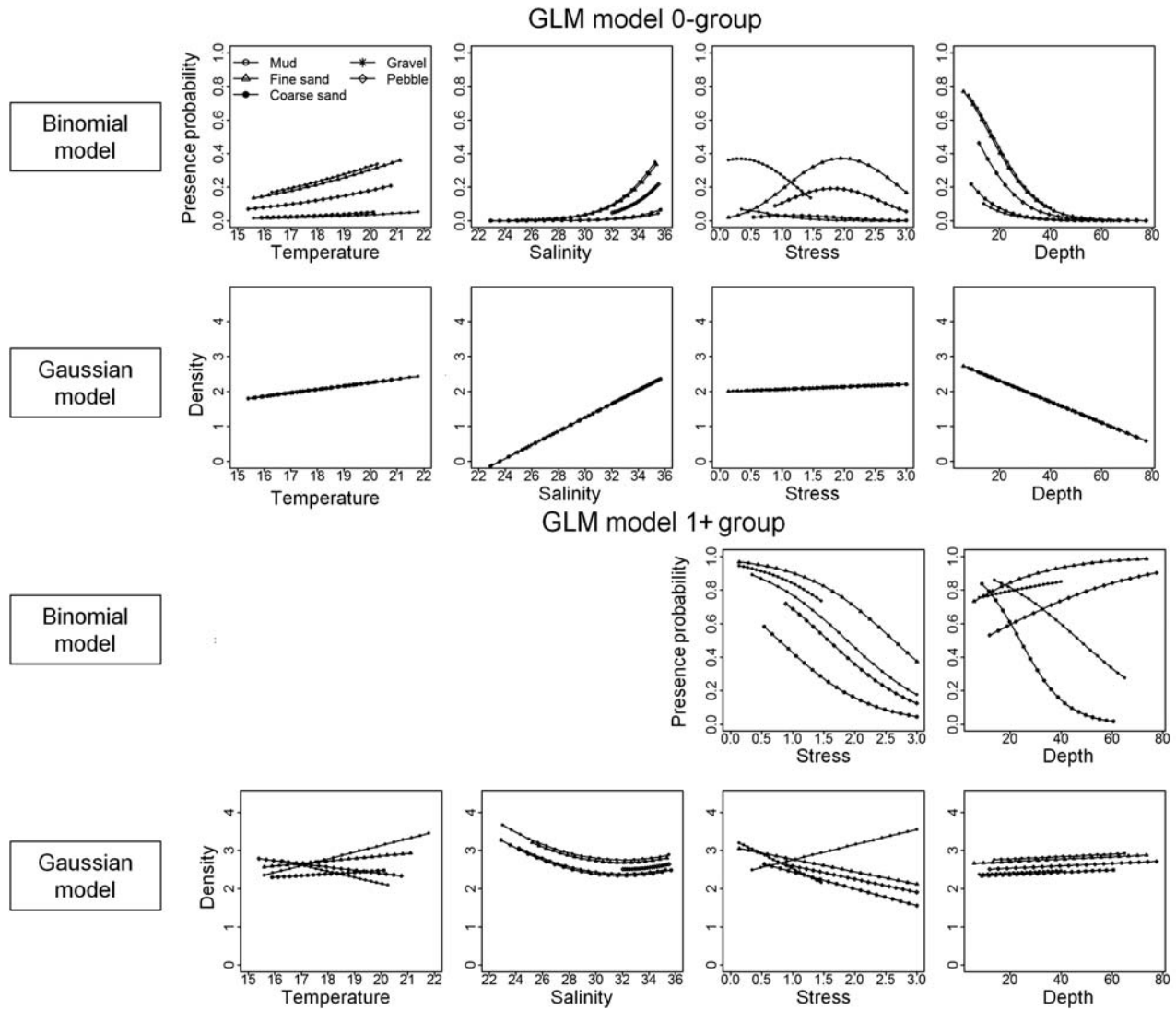
Figure 3. Predicted densities as a function of the significant explanatory variables for the GLM binary and Gaussian models in July/August for 0-group and 1+ group plaice. Each plot illustrates the response along a given environmental gradient, with all other variables remaining constant at their mean value. When significant, the effect of each sediment type is plotted as separate lines.

plaice in the eastern English Channel over two seasons. Coefficients of determination for final models ranged from 0.13 to 0.81, higher values indicating better model fit for autumn (0.13–0.81) than for summer (0.13–0.3) for both age groups and both modelling approaches (Table 1). Hence, the tested environmental variables had less predictive power for the spatial distribution of 0-group and 1+ plaice in summer. For both GLM models and QRs, depth and temperature were always significant, so were structuring plaice habitat at both seasons and life stages considered. In summer, 0-group plaice showed an affinity for mud and fine sediments and shallow water, in contrast to the 1+ group which was found mainly on coarser sediments in summer and finer muddy sediments in autumn (Figures 3–5). As a result of first-order interaction between the continuous variables and sediment type, the form of certain species responses varied with sediment type. The 0-group showed a negative relationship with depth in most models, whereas the relationship between older fish (1+ group) and depth varied depending on the sediment type on which they occurred. Young plaice (0-group)

exhibited a strong preference for fine sediment such as mud and fine sand, unlike older fish (1+ group), which preferred coarse (mainly pebble and gravel) sediments. This was reflected in the pattern of distribution of the two life stages. Indeed, during summer, younger fish preferred shallow water with low to intermediate tidal currents, whereas older fish were distributed more widely. In autumn, the distribution pattern contracted along the coasts, and the potential habitat model illustrated the affinity of the species for sandy to gravelly sediment types. The relationship with temperature seemed to switch between the two seasons, with a negative or trough-shaped relationship in autumn and a positive relationship in summer. This is particularly true for the 0-group in summer, as shown by the GLM (Figure 3) and the QR model (Figure 5). The effects of salinity and bed stress on juveniles were weak, showing a slightly positive effect of high salinity in summer and a negative effect of bed stress in both seasons (Figures 3–5). This positive effect of salinity, owing to a very minor interaction with depth, was not found in the QR.
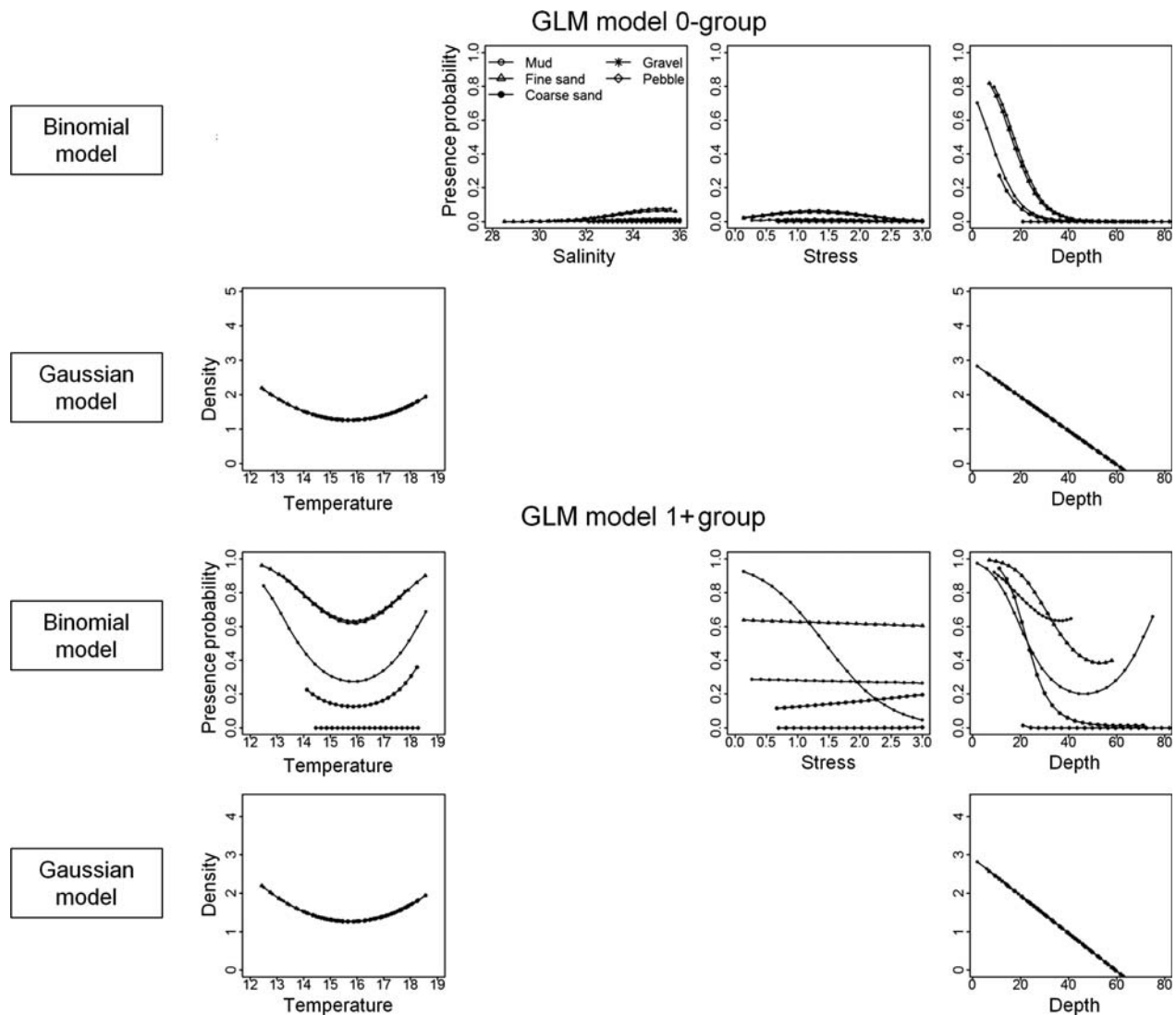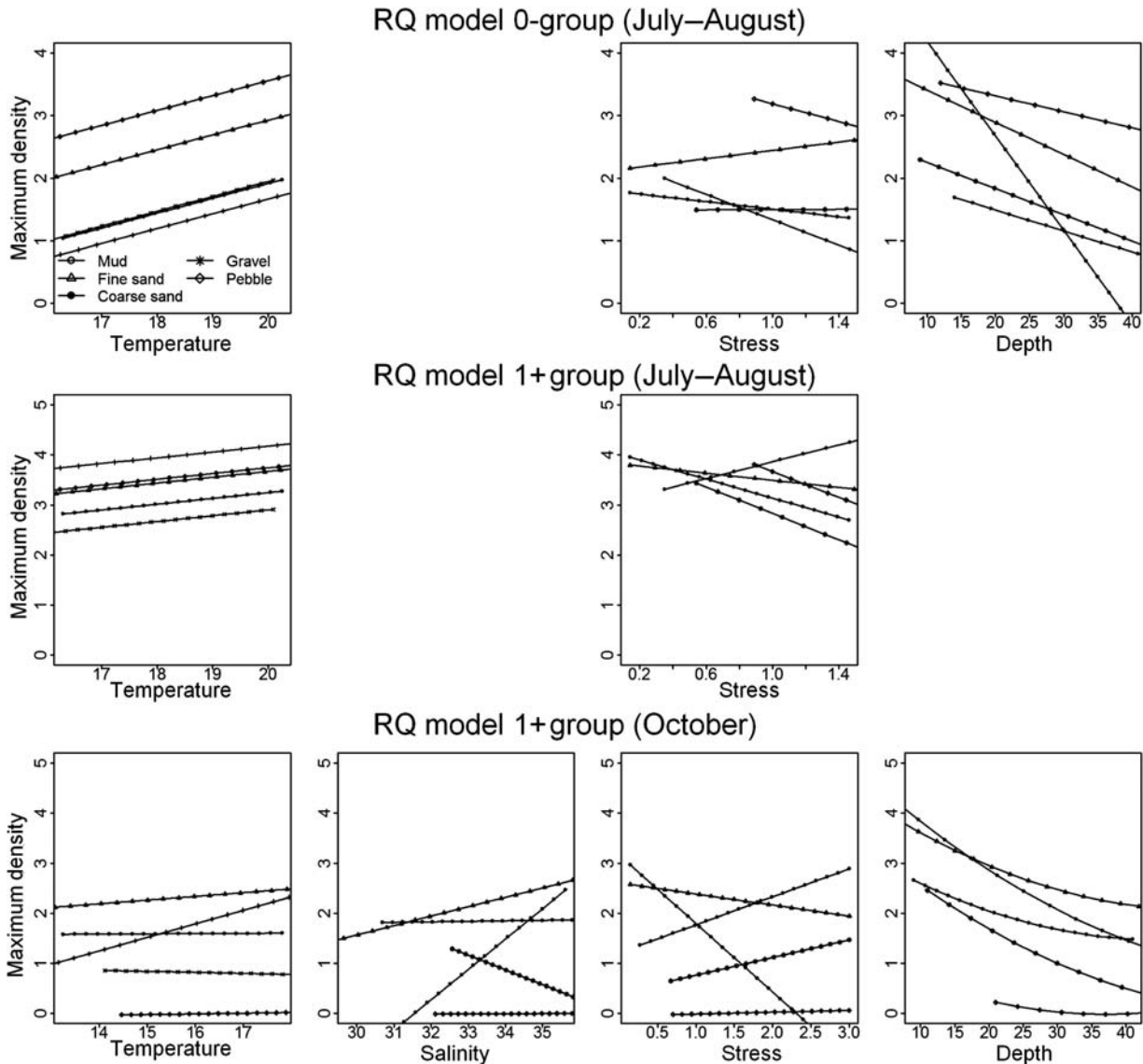
Figure 4. Predicted densities as a function of the significant explanatory variables for the GLM binary and Gaussian models in October for 0-group and 1+ group plaice. Each plot illustrates the response along a given environmental gradient, with all other variables remaining constant at their mean value. When significant, the effect of each sediment type is plotted as separate lines.

Predicting the spatial distribution of plaice and its uncertainty

The mapped predicted plaice densities for the finally selected models were fairly consistent across modelling approaches, in particular for the 1+ group (Figure 6). Corresponding maps of uncertainty showed that delta-GLM predictions were more uncertain than the QR approach for which predictions were only locally highly uncertain (Figure 7). The predicted spatial distributions were coherent with the distributions obtained directly from the CGFS and BTS data (as an average across 1988–2006 for BTS and 1989–2006 for CGFS; Figure 8). Predicted density maps based on QR models, which represent potential habitats, were usually more optimistic, i.e. covering larger surface areas, than distributions predicted with the delta-GLM models that corresponded to preferential habitats.

In July, 0-group preferential habitats (Figure 6a) were close to the coast, near estuaries on both French and British coasts, and prediction uncertainty was greater at the coasts but low in the central areas, suggesting almost no uncertainty about the spatial extent of areas where the species was absent (Figure 7a). The potential habitat model highlighted coastal areas extending offshore as favourable (Figure 6e). For those predictions, the error was almost null across the region except in the southwest, where it was high (Figure 7e). In October, 0-group preferential habitat was spatially more restricted than in July, encompassing coastal areas close to estuaries (Figure 6c). The corresponding potential habitat map was similar to the preferential one, but it exhibited a more dispersed offshore spatial distribution in the Straits of Dover and the southern North Sea (Figure 6g). Older fish (1+ group) were generally found in the same areas as younger ones, but had a more offshore distribution pattern. In July, the 1+ group preferential habitats were found across the Straits of Dover, in the southern North Sea, and in the bays of the rivers Seine and Veys. There were no fish in the central Channel where the water is deeper. The potential habitat maps indicated favourable habitats farther offshore. In October, the distribution

RQ model 0-group (July–August)

RQ model 1+group (July–August)

RQ model 1+group (October)

Figure 5. Predicted maximum densities as a function of the significant explanatory variables for QR models in July/August and October for 0-group and 1+ group plaice. Each plot illustrates the response along a given environmental gradient, with all other variables remaining constant at their mean value. If seabed sediment type was a significant predictor of the model, the effect of each sediment type on the response is plotted as lines.

pattern of both preferential and potential habitats contracted along the coasts, though the preferential habitat was very uncertain (Figure 7).

Model evaluation

For all final models, there was a strong and significant positive correlation (Spearman's correlation test) between observed and predicted density values (Table 2). This was confirmed by the plot of observed values against model-predicted values (Supplementary Figure S1). The Wilcoxon signed-rank test for GLMs revealed a weakness of the models in predicting realistic density levels (Table 2). The results of the CC test (for QR models) suggested that those models performed relatively well, predicting the correct proportion of values higher than the model's quantile (Table 2).

Discussion

In marine ecosystems, environmental factors play an important role in determining fish distributions. In previous studies, flatfish distributions have only been related to single environmental factors (Smale *et al.*, 1993; Albert *et al.*, 1998; Ellis *et al.*, 2000; Amezcua and Nash, 2001), but the models developed here contained the explanatory variables sea surface temperature, bed-shear stress, salinity, depth, and seabed sediment type (sands, gravels, and mixed substratum). For both summer and autumn, habitat models showed that the predicted distribution of 0-group plaice was more coastal than that of the 1+ group, which spread farther offshore, confirming the results of previous studies conducted in the English Channel (Riou *et al.*, 2001). This distribution pattern seems to be specific to the eastern English Channel and may be explained by the abiotic factors of
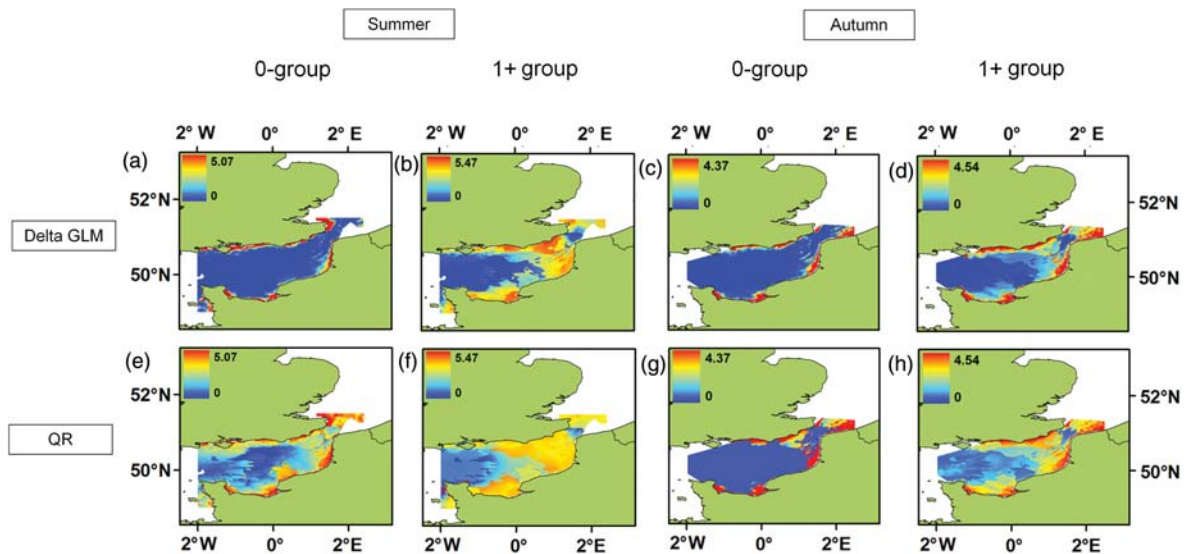
Figure 6. Predicted (delta-GLM) population density ($\log_{10}$-scale) representing preferential habitat for (a) 0-group and (b) 1+ group plaice in July/August, and (c) 0-group and (d) 1+ group plaice in October. Predicted (QR-95 model) population density ($\log_{10}$-scale) representing potential habitat for (e) 0-group and (f) 1+ group plaice in July/August, and for (g) 0-group and (h) 1+ group plaice in October.
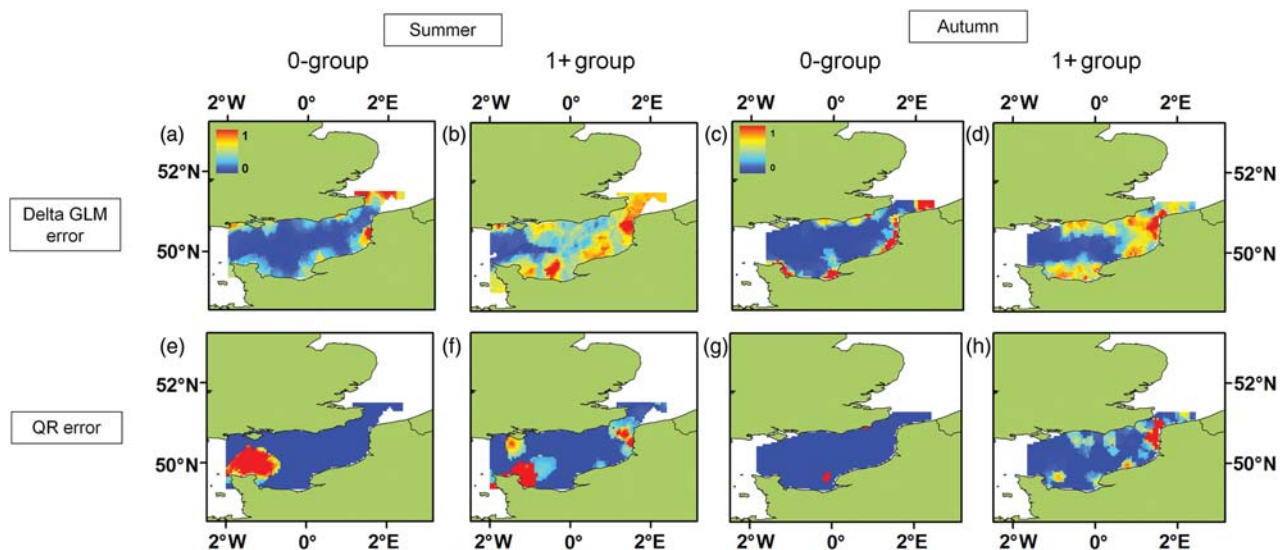
Figure 7. Spatialized uncertainty (error) of preferential and potential habitat maps in Figure 6. Delta-GLM for (a) 0-group and (b) 1+ group plaice in July/August, and (c) 0-group and (d) 1+ group plaice in October. QR-95 model for (e) 0-group and (f) 1+ group in July/August, and (g) for 0-group and (h) 1+ group in October.

the area (Carpentier *et al.*, 2009). Others have noted this different pattern between juvenile and adult plaice in the North Sea, where 0-group are normally found in shallow water, but then move gradually offshore as they grow. Surveys in the Wadden Sea, however, have demonstrated that 1-group plaice are almost absent from the area where they once were very abundant. This is probably linked to changes in the productivity of the region, but also to the changing temperature of the southern North Sea (van Keeken *et al.*, 2007).

Environmental variables

Water temperature tends to be the main factor explaining seasonal movements of flatfish between onshore and offshore habitats,

principally in shallow water where temperature fluctuations are greater than in deeper water (Gibson, 1997). Overall, water temperature in the study area is closely linked to bathymetry, with the warmest water found shallow in summer, and deeper in winter (Carpentier *et al.*, 2009). Tidal currents are also strong in the area, and they enhance water mixing at moderate depths throughout the year (Hoch and Garreau, 1998). These environmental conditions were reflected in the different habitat preference of young and adult plaice. In fact, bed-shear stress limited mainly adult habitat selection. In addition, the coastal distribution of juveniles was strongly positively related to water temperature and bed-shear stress in summer, demonstrating that young plaice prefer shallow warmer water.
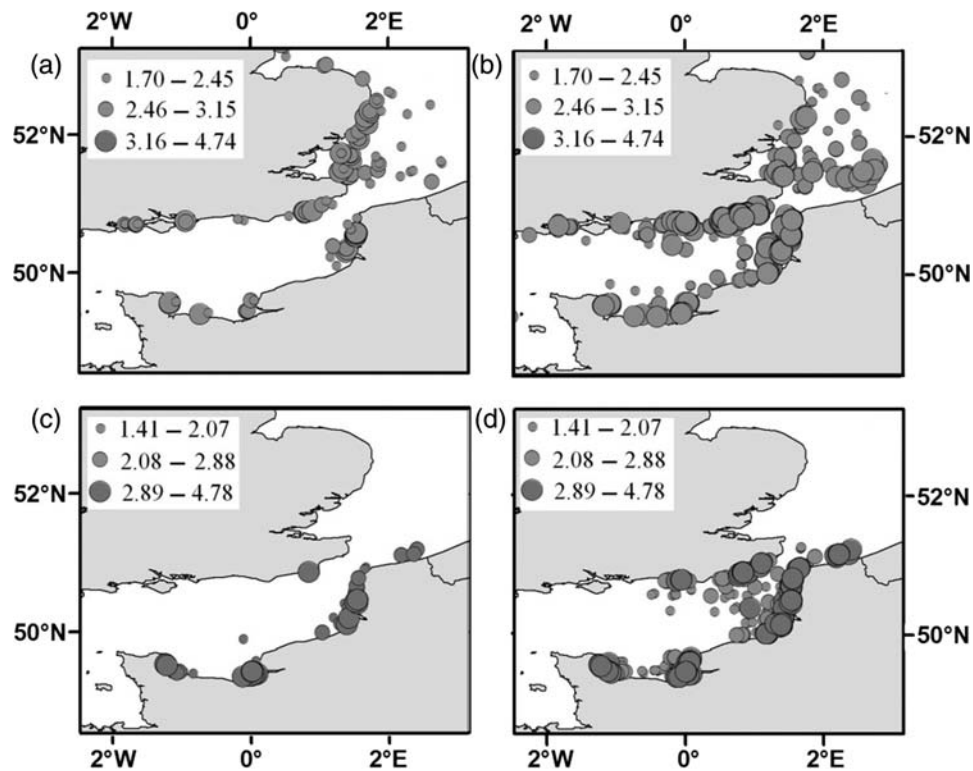
Figure 8. Survey density ($\log_{10}$-scale) distribution maps: (a) 0-group, (b) >1+ group plaice in July/August (BTS 1988–2006); (c) 0-group, (d) 1+ group plaice in October (CGFS survey 1988–2006). Maps were created by averaging across years for each survey.

Table 2. Model evaluation results using the bootstrapping procedure.

Period	Model	Life stage	Spearman correlation		Wilcoxon test		
			r_s	*p*-value	W+	*p*-value	CC test
July/August	Delta-GLM	0-group	0.48	***	206 675	(<0.05)	
		1+ group	0.61	***	385 459	(<0.05)	
	QR	0-group	0.44	***			95.34
		1+ group	0.46	***			95.34
October	Delta-GLM	0-group	0.48	***	101 063	(<0.05)	
		1+ group	0.69	***	216 556	(<0.05)	
	QR	0-group	0.35	***			97.14
		1+ group	0.66	***			88.93

CC test, correct classification test. Values in parenthesis indicate that the test failed. Spearman's correlation coefficient (r_s), *p*-value < 0.001 (***); Wilcoxon test (W+), *p*-value >0.05 (***).

The coastal distribution of young fish may also be driven by predation, which is size-dependent with younger stages suffering greater mortality (Power, 1987). Shallow water increases the protection from predation and any factor that increases growth rate will reduce predation vulnerability. In summer, warmer coastal waters are likely to favour faster growth, so influencing the coastal distribution of young plaice (Gibson *et al.*, 2002). Both preferential and potential habitat maps reflected this difference. The relationship with temperature, however, was not as strong and clear in autumn as in summer. Adult plaice seemed to have a more offshore distribution and less affinity for warm water than younger stages. Fonds *et al.* (1992) hypothesized that large fish are less dependent on warm water for faster growth than smaller fish. Such a relationship was confirmed for adult plaice in the potential habitat models, showing that temperature can have a

limiting effect on habitat selection in combination with different sediment types. The preferential habitat model, however, showed no clear relationship between water temperature and habitat selection.

Substratum type was the most important predictor in explaining plaice spatial distribution, especially during the early life stage. Juvenile plaice are strongly habitat-specific during their early benthic stage, with juvenile plaice occupying selected sediments preferentially based on grain size (Gibson and Robb, 2000). This situation is determined principally by the ability of fish to bury in the sediment, food abundance, and by the necessity to shelter from predators (Gibson, 1994; Stoner and Abookire, 2002). In accord with this, 0-group plaice showed a preference for fine sediments (fine sand and mud) in both seasons and both model types, with some fish living on pebbles during summer. Finer sediments

have the advantage of requiring less energy for burying, which has a clear survival advantage (Gibson and Robb, 1992). In contrast, adult fish seem to prefer coarser sediments.

Plaice undergo an ontogenetic change in diet as they grow, and this may explain the different distribution patterns found between adults and juveniles (Piet *et al.*, 1998). Juveniles feed mainly on infaunal polychaetes and bivalves, whereas adults take a large proportion of epibenthic crustaceans, small fish, and echinoderms (Piet *et al.*, 1998). Also, sediment type plays a major role in the spatial distribution of benthic invertebrates, perhaps explaining the wider distribution of plaice in summer, when there is probably more food immediately available in the area. Our results agreed with those of earlier studies (Gibson *et al.*, 1996) in showing that plaice distribution remains relatively stable throughout the year, although it may change/evolve in summer through movements towards deeper water, as a result of prey availability.

In agreement with the findings by Creutzberg *et al.* (1978), salinity changes had no effect on the spatial distribution of plaice of either life stage or season. Also, there was no marked evidence of salinity limiting habitat selection. Although our predicted habitat maps agreed with earlier findings, the resulting models remained complex and did not isolate a single environmental variable effect.

Methodology

Predicting and modelling fish habitat distributions require good knowledge of abiotic factors on a fine spatial scale. The five environmental variables tested here have indirect and overlapping effects on fish distribution and may share a substantial amount of variation. This generally results in overfitted models that may predict the spatial distribution adequately without necessarily identifying the underlying driving factors (Loots *et al.*, 2010). To overcome this problem, Loots *et al.* (2010) suggested model selection based on predictive performance rather than model goodness of fit.

The GLM evaluation (Wilcoxon's signed-rank test) revealed that this two-step approach predicted the presence/absence distributions better than density levels. Species distribution models are restricted to modelling species response to the environment, which alone cannot be expected to explain the spatial distribution of fish populations, unless it is very strong. Biotic mechanisms are expected to affect spatial distribution too. Loots *et al.* (2010) showed for North Sea spawning plaice that temporal changes in the spatial distribution seemed to be primarily influenced by population size and demography. In that study, variations in hydrographic conditions such as temperature and salinity did not appear to control interannual fluctuations in spatial distribution. The importance of density-dependent effects has also been demonstrated for small pelagic fish (Planque *et al.*, 2011) and other flatfish species concomitant with environmental effects (Spencer, 2008). Density-dependent or demographic effects were not tested here because the main aim was to investigate plaice spatial distribution in response to environmental variables.

Two types of approach were used here. GLMs are expected to give more realistic predictions than QR models, which model the upper bound of the density distribution and therefore overestimate local species densities. In contrast, with QR models, the effects of limiting factors on species distributions can be studied. The use of both modelling approaches is basic to answering contrasting ecological questions regarding fish habitat selection.

Supplementary material

Supplementary material is available at the *ICESJMS* online version of this manuscript. Table S1 provides metadata for BTS and CGFS surveys, and Figure S1 shows observed values plotted against model-predicted values.

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