

A digital atlas to link ontogenic shifts in fish spatial distribution to the environment of the eastern English Channel. Dab, *Limanda limanda* as a case-study

by

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ABSTRACT. - The eastern English Channel, which connects the Atlantic Ocean to the North Sea through the Dover Strait, is an area where numerous and often conflicting human activities take place. A cross-border multidisciplinary project called CHARM was initiated to provide knowledge and tools for planners and decision-makers to durably manage the shared marine living resources. One such tool was an atlas of fish spatial distributions and modelled habitats, which was used here to investigate ontogenic and seasonal shifts in fish spatial distribution and habitat through a case-study, the dab *Limanda limanda*. Survey data for several life-history stages (eggs, larvae, coastal nurseries, < and > 1 year old) and seasons were used to map spatial patterns (using geostatistics), and model potential habitats (using regression quantiles) based on environmental predictors. Habitat models were generally consistent with surveyed spatial patterns and helped explaining dab response to its environment. Dab response to hydrological parameters (e.g., temperature, salinity) was more variable (depending on the life stages and seasons considered) than response to physical parameters (e.g., depth, bed shear stress, seabed sediment type). The results of this work contribute to a better understanding of this species spatial ecology in the eastern English Channel.

RÉSUMÉ. - Atlas numérique permettant de relier les distributions spatiales des différents stades de vie de poisson à l'environnement de Manche orientale. L'exemple de la limande *Limanda limanda*.

La Manche orientale, qui relie l'océan Atlantique et la mer du Nord par le Détroit du Pas-de-Calais, est une zone où de nombreuses et souvent antagonistes activités humaines ont lieu. Le projet international et pluridisciplinaire CHARM a été initié afin de fournir les connaissances et outils nécessaires aux gestionnaires et décideurs, pour une gestion durable des ressources marines vivantes de cette région transfrontalière. L'un de ces outils a pris la forme d'un atlas des distributions spatiales et des habitats de poisson. Il est utilisé ici pour étudier la saisonnalité des distributions spatiales et des habitats à travers les stades ontogéniques d'une espèce type : la limande *Limanda limanda*. Des données de campagnes sur plusieurs stades de vie (œufs, larves, nurseries côtières, < et > 1 an) et saisons ont été utilisées pour cartographier (avec les géostatistiques) les distributions spatiales et modéliser (avec les régressions quantiles) les habitats potentiels à partir de paramètres environnementaux. Les modèles d'habitats étaient généralement cohérents avec les distributions spatiales et ont permis de mieux comprendre les relations de la limande avec son environnement. Ses relations avec les paramètres hydrologiques (ex. température, salinité) étaient plus variables (dépendantes des stades de vie et des saisons) qu'avec les paramètres physiques (ex. profondeur, tension de cisaillement sur le fond, type de sédiment de fond). Les résultats de cette étude contribuent à une meilleure compréhension de l'écologie spatiale de la limande en Manche orientale.

Key words. - Pleuronectidae - *Limanda limanda* - Eastern Channel - Spatial distribution - Modelling - Kriging - Ichthyoplankton - Trawl - CUFES.

The English Channel (Fig. 1) is a shallow epicontinental sea bordered by the United Kingdom and France. It connects the Atlantic Ocean to the North Sea via the Dover Strait. A number of commercial marine species (fish, shellfish) can be found there, as well as spawning, nursery and feeding areas,

migration routes for fish, birds and marine mammals. The eastern English Channel is a strategic area in north-western Europe as it represents a significant economic zone where a number of, often conflicting, human activities take place: tourism and leisure, international ports and freight, the

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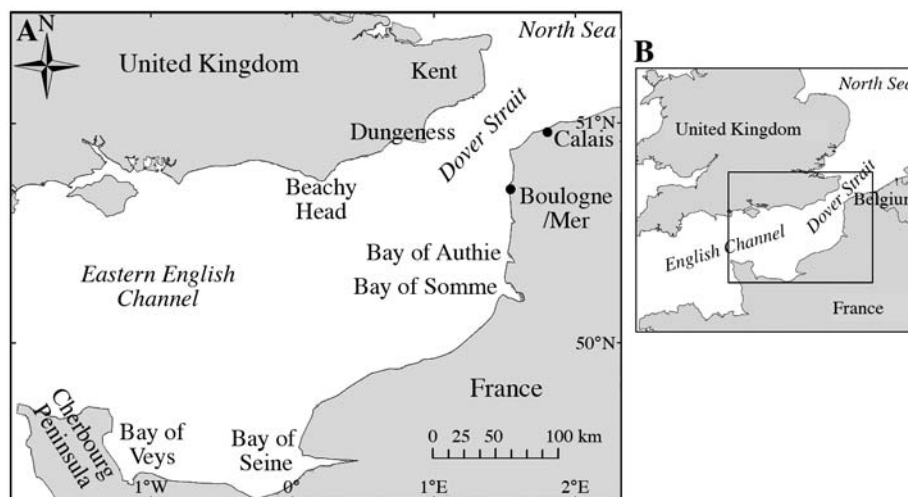


Figure 1. - **A, B**: Study area of the CHARM project. Locations mentioned in the text are shown.

exploitation of living (e.g., fisheries) and non-living (e.g., mineral) resources, development of offshore wind farms, installation of submarine cables (Carpentier *et al.*, 2009). In this context, the multidisciplinary CHARM (Channel Habitat Atlas for marine Resource Management) project aimed, through a number of objectives, to increase the knowledge of this marine cross-border area and to provide tools for planners and decision-makers to better manage it (Martin *et al.*, 2009). One such tool was an atlas of marine resources and modelled habitats in the eastern English Channel (the “CHARM Atlas”, Carpentier *et al.*, 2009), which will be used here, through a case study, to investigate ontogenic and seasonal shifts in fish spatial distribution and habitat.

Limanda limanda Linnaeus, 1758, or dab, is a north-east Atlantic demersal species found between 20 and 150 m depth (Frimodt, 1995). This flatfish is dominantly benthivorous, although larger individuals occasionally feed on small demersal fish (De Clerck and Torreele, 1988). This species, presented here as an example of the results that can be obtained using the information and maps in the CHARM Atlas, was selected for several reasons. It is common in the English Channel (Parker-Humphreys, 2005; Carpentier *et al.*, 2009) and very abundant in the nearby southeastern North Sea (Daan *et al.*, 1990) where it is notably used for ecotoxicological research and environmental monitoring (pollution) programs (Rijnsdorp *et al.*, 1992). There is no on-going stock assessment by the International Council for the Exploration of the Sea (ICES) for this species despite it being a bycatch species with unevaluated discards at sea. For this reason, scientific survey data (as presented here) are essential to its monitoring. Further, it is a prey item for numerous predator species such as seals, various sharks and rays, gadoids, gurnards and some flatfish (Mackinson and Daskalov, 2007), many of which are commercially exploited

(e.g., whiting, cod) or vulnerable to exploitation (sharks and rays).

The spatial distributions of fish life-history stages can be superimposed on oceanographic features (Harden-Jones, 1968). In the present study, habitat was defined as waters and substrates necessary for fish growth, reproduction, survival and feeding (USDC, 1997). To model a species’ habitat, regression methods can be used to provide numerical estimates of how the species responds (e.g., in terms of abundance) to changes in one or more environmental factors. The majority of species distribution modelling approaches are currently based on an estimation of mean or median (central tendency) species response to environmental factors (Oksanen and Minchin, 2002). In contrast, Regression Quantile (RQ) modelling (Cade and Noon, 2003) estimates the effect of limiting environmental factors on the species response, hereby delineating its maximal or “potential” habitat (i.e., all possible areas with conditions suitable for species presence or high abundance levels). Predictions from upper RQ models (typically modelling abundance between the 0.75 and 0.95 quantiles) are less likely to underestimate species responses’ to the environment, hence the value of the habitat, and therefore have potential benefits for precautionary management of living resources (Vaz *et al.*, 2008).

Rijnsdorp *et al.* (1995) stated that “it is obvious that the quality and quantity of [flatfish] habitat available to the successive life-history stages may have a profound effect on the number of a cohort that may successfully close the life cycle”. High-resolution spatial distributions and modelled habitats for several life-history stages (from egg to adult stage) and seasons are herein presented and interpreted for dab. The purpose of the work presented here is to contribute to a better understanding of this species spatial ecology in the eastern English Channel.

MATERIALS AND METHODS

Sea surveys

For a number of fish species, including dab, relative abundance (or densities, noted x) were available for each of the main life-history stages (Table 3 in Martin *et al.*, 2009, summarises data availability per life-history stage for the 33 fish species considered in the CHARM project). Out of the datasets used, data on early life-history stages (pelagic eggs and larvae) were relatively limited (in terms of survey surface areas and time scales) compared to those on other developmental stages (demersal juveniles and adults) for which identification is less time and labour intensive. Early life-history stages show, however, the highest natural mortality in the fish life cycle and tend to be less understood than older life-history stages. The datasets used here were:

Egg surveys: IBTS 2007

At the end of January 2007 during the French IBTS (International Bottom Trawl Survey), pelagic fish eggs were sampled in parts (Fig. 2A) of the eastern English Channel using a Continuous Underway Fish Egg Sampler (CUFES; Checkley *et al.*, 1997) equipped with a 500 μm mesh-size net. A total of 179 samples provided real-time estimates (over 30 min

sequential intervals) of the volumetric abundance of pelagic fish eggs (standardised as number of individuals per 20 m^3 , or nb.ind./20 m^3 , of water filtered) at pump depth. Eggs were then identified by species and developmental stage (Russell, 1976; Munk and Nielsen, 2005), though only data on stage 1 eggs (which do not yet have a visible embryo) were used in subsequent data analyses. Stage 1 eggs are believed to be closest, in time and space, to the original spawning location: spawning areas may therefore be inferred from the distribution of stage 1 eggs.

Larval surveys: REISE 1 and 2, 1995; BCD 1999

Fish larval data were collected during three surveys: REISE (“Distribution of ichthyoplankton between the Scheldt and Seine estuaries”) 1 (Apr. 1995, 45 samples) and 2 (May 1995, 60 samples), and BCD (“Biodiversity and Cartography throughout the Dover Straits”, Apr. 1999, 39 samples) (Fig. 2B; Grioche *et al.*, 1999 and Koubbi *et al.*, 2006). Ichthyoplankton was sampled with a double-framed bongo net (plankton nets of 500 μm mesh size), during diagonal tows at a speed of 2 knots, from the surface to the proximity of the seabed. Samples were then analysed to identify larval species (according to Russell, 1976) and developmental stages. These stages were defined by morphological and pigmentation

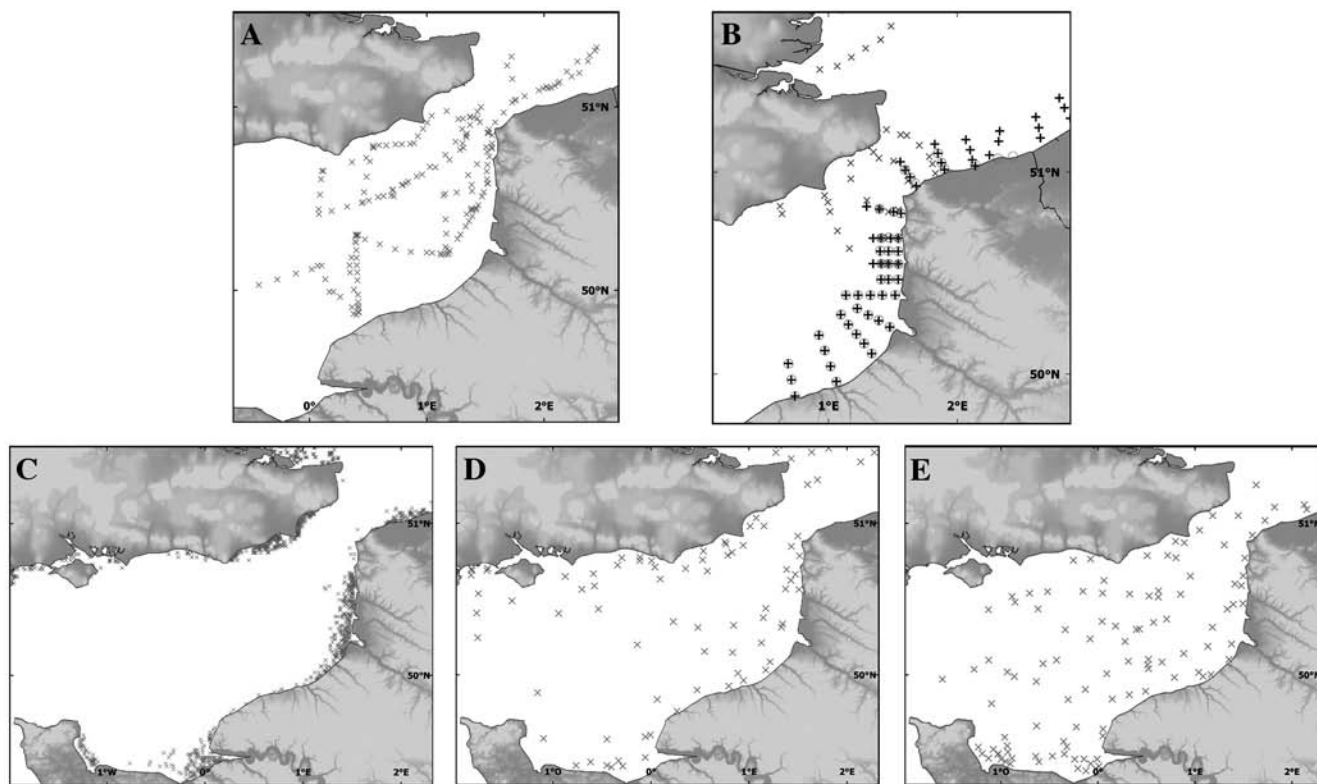


Figure 2. - Sampling stations for A: the IBTS (egg survey, x , January 2007), B: the REISE (+, o, April and May 1995) and BCD (x , April 1999) larval surveys, C: the YFS (coastal nursery surveys, x , September 1977-2006), D: the eastern Channel BTS (larger-scale trawling surveys, x , July/August 1989-2006; 2006 as an example), and E: the CGFS (larger-scale trawling surveys, x , October 1988-2006; 2006 as an example).

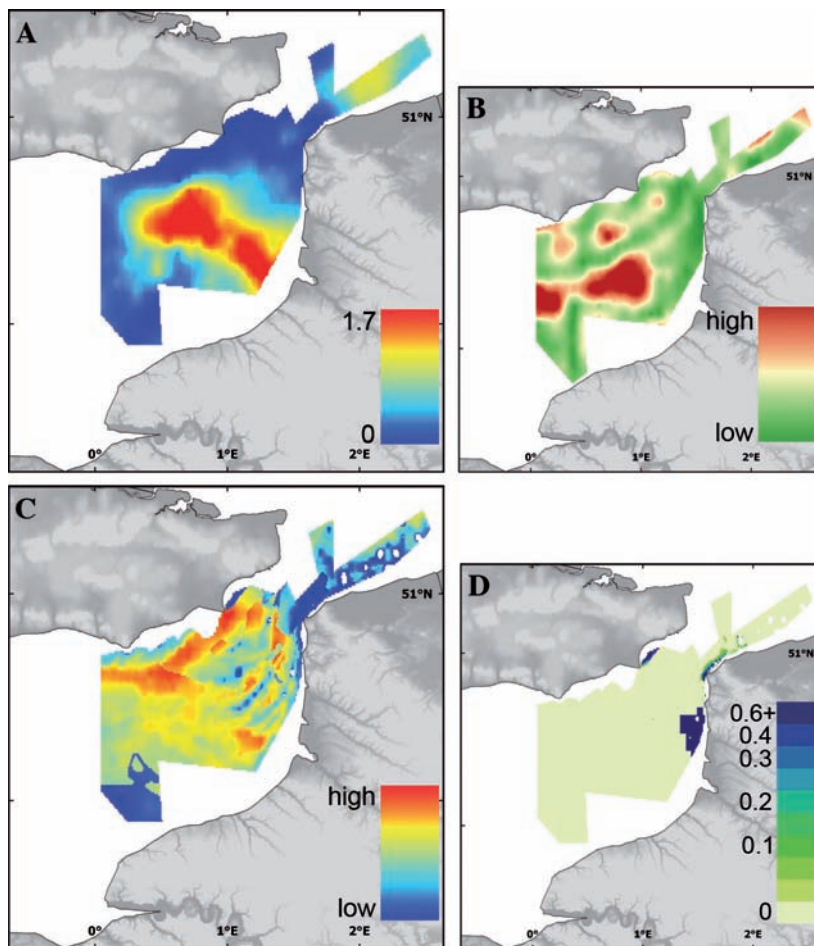


Figure 3. - *Limanda limanda* stage 1 eggs. **A:** Spatial distribution of abundance ($\text{Log}_{10}[x+1]$, $x = \text{nb. ind.}/20 \text{ m}^3$) in January; **B:** Kriging error; **C:** Potential habitat in January; **D:** Model error.

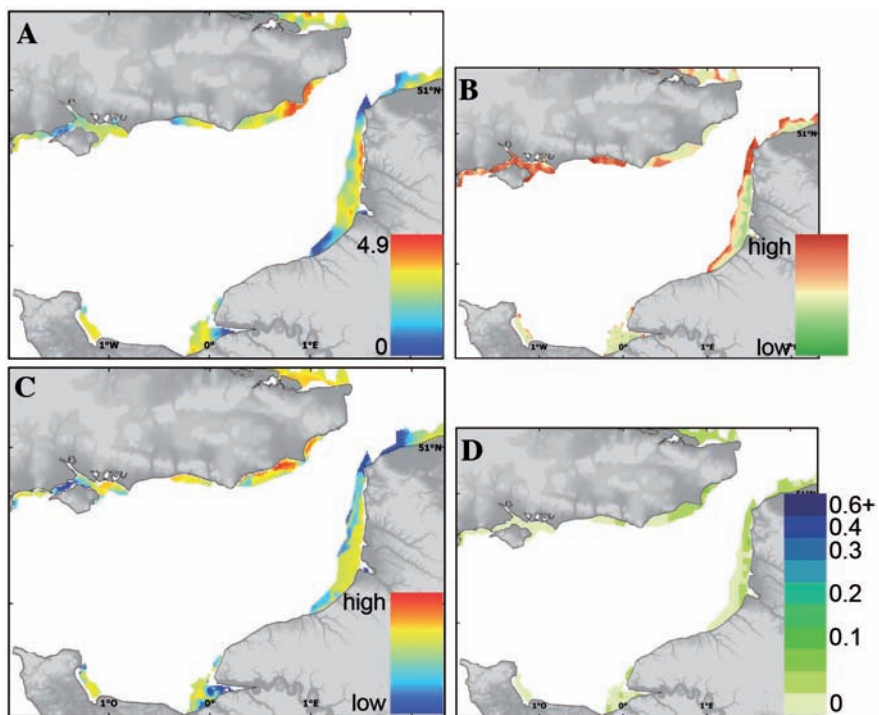


Figure 4. - *Limanda limanda* (essentially juveniles) in coastal nurseries. **A:** Multi-annual spatial abundance ($\text{Log}_{10}[x+1]$, $x = \text{nb. ind.}/\text{km}^2$) distribution in September; **B:** Kriging error; **C:** Potential habitat in September; **D:** Model error.

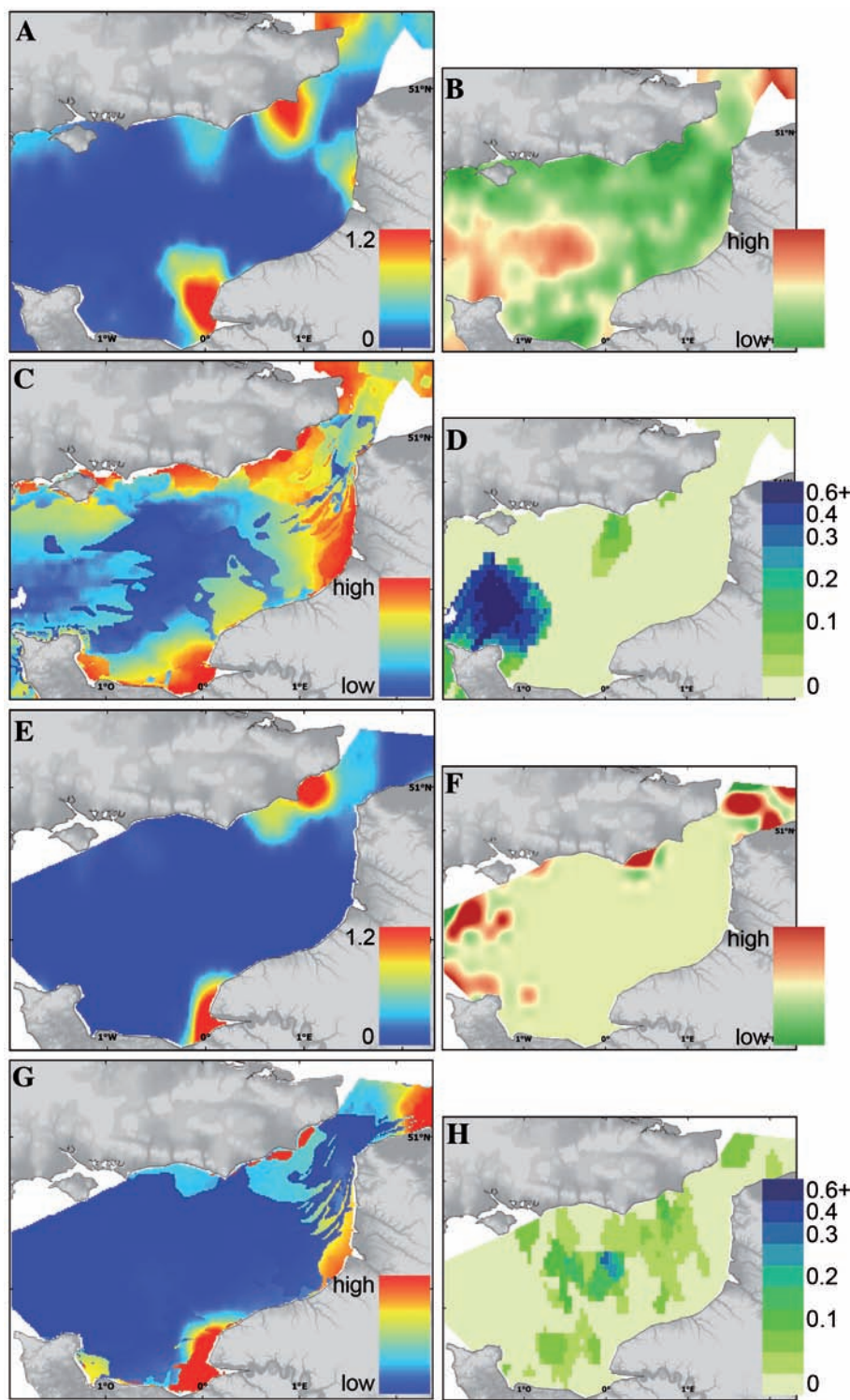


Figure 5. - *Limanda limanda* 0-group. **A:** Mean spatial distribution of abundance ($\text{Log}_{10}[x+1]$, $x = \text{nb. ind./km}^2$) in July/August; **B:** Kriging error; **C:** Potential habitat in July/August; **D:** model error; **E:** Multi-annual spatial distribution of abundance in October; **F:** Kriging error; **G:** Potential habitat in October; **H:** Model error.

tion patterns adapted from Ryland (1966) as: yolk-sac larvae (stage 1); pre-flexion larvae, i.e., feeding on prey and no

longer on their yolk (stage 2); post-flexion larvae with the formation of dorsal and anal fins (stage 3); transition larvae with all fin rays formed (stage 4); eye migration and metamorphosis (stage 5, for flatfish). In the present study, the term larva was used until metamorphosis takes place, after which (and until maturity is reached) the term juvenile was used. Larval volumetric abundance was standardised as the number of individuals per 100 m^3 of water filtered ($\text{nb.ind./}100 \text{ m}^3$).

Coastal nursery surveys: YFS 1977-2006

The dataset considered here gathers data from a number of coastal beam trawl Young Fish Surveys taking place in September, on both the French (1977-2006) and UK (1981-2006) coasts. Depending on the year considered, the extent of the areas surveyed varied considerably. The methodologies of the French (Riou *et al.*, 2001) and UK (Rogers *et al.*, 1998a) surveys were similar enough for their data to be standardised so as to take into account, for example, differences in gear characteristics (trawl width, number of chains, mesh size). With standardised abundance data (being expressed in numbers of individuals per km^2 , or nb. ind./km^2), there was a good coherence in catch rates where French and British YFS coincided (Vaz *et al.*, unpubl. results). As fish length data were not available for all the datasets used, the results refer to individuals of all sizes, though essentially juveniles. French (1,441 trawl hauls) and UK (3,784 trawl hauls) data were combined and averaged over all the available time series and spatial extent (Fig. 2C).

Larger-scale trawling surveys: BTS 1989-2006 and CGFS 1988-2006

The eastern Channel Beam Trawl Survey (BTS) has been conducted each July/August, since 1989 (Parker-Hum-

phreys, 2005). It uses a commercial 4 m beam trawl, towed for 30 minutes at a speed of 4 knots, sampling at about 100 stations (Fig. 2D). The trawl has a 40 mm codend liner to retain small fish, and fishing is only carried out in daylight, as the vertical distribution of some species is known to vary diurnally. At each sampling station, fish (adults and juveniles) species were sorted, weighed, counted, measured and (when relevant) sexed. Abundance data from a total of 1,849 trawl hauls including some in the southern North Sea, north-east of the study area (out of the CHARM study area), and for 25 fish species, were expressed as density in nb.ind./km².

The Channel Ground Fish Survey (CGFS) has taken place annually in the eastern English Channel each October since 1988 (Coppin *et al.*, 2001). The sampling gear was a Very High (~ 3 m) Vertical Opening (VHVO) bottom trawl (or "GOV"), well adapted for catching demersal species, with a 10 mm mesh size in the codend for capturing juveniles. One or two 30 minutes hauls were performed at 90-120 stations (Fig. 2E), at an average speed of 3.5 knots. At each sampling station, fish (adults and juveniles) species were sorted, weighed, counted, measured and (when relevant) sexed. Abundance data from a total of 1,647 trawl hauls and for 31 fish species were expressed as density in nb.ind./km².

Data analyses

Survey abundance data were tested for normality (using histograms, skewness and kurtosis) and usually needed to be log-transformed ($\text{Log}_{10}[x+1]$) so as to improve their distribution normality.

Estimation of length at one year old

Although for many species, individuals are not considered as mature adults at one year old, they are nonetheless generally able to reach and feed on the same habitat as older fish. Juvenile fish of < 1 year, however, may be more limited in their swimming and competitive abilities and may be confined to different areas. For BTS and CGFS survey data, the distinction between < 1 year old (i.e., "0-group") individuals and older ones was based on length (L_1) at one year old

(T_1), which was estimated using the von Bertalanffy growth function (von Bertalanffy, 1938). Dab reaches maturity at $T_m = 2.3$ year old for a length of $L_m = 13$ cm, mean asymptotic length being $L_\infty = 27$ cm (Rijnsdorp *et al.*, 1992).

Interpolation of survey data using geostatistics

Geostatistics embody a suite of methods for analysing spatial data and for their interpolation (Webster and Oliver, 2001). It is basically a set of methods for estimating the values of a property of interest at non-sampled locations, from more or less sparse available sample data points for this variable. Kriging, one of the geostatistical interpolation methods, was used to estimate each species' densities on a regular grid of latitudes and longitudes coincident with the areas sampled during the surveys considered. The grid of estimated densities was then smoothed within a Geographical Information System (GIS) to produce continuous spatial distribution maps of the various life-history stages considered. Vaz *et al.* (2005) and Carpentier *et al.* (2009) describe, in detail, the methodologies followed to produce these maps.

Mean maps correspond to the average of each year's spatial distribution for a time period, whilst multi-annual maps were constructed using data pooled over a time period. The latter was used when data were not adequate for mapping each year separately, e.g., when species occurrence was infrequent, or when the sampling gear used did not catch a species representatively (e.g., GOV trawl and 0-group dab). The map of kriging error (or estimation variance) shown against the interpolated spatial distribution map illustrates the quality of kriging estimation. In the case of mean maps, the kriging error was computed as the sum of the kriging error of each year's maps. The survey spatial patterns for dab larvae can be found in Koubbi *et al.* (2006), and are not presented here.

Potential habitat modelling using regression quantiles

The methodologies followed were described by Vaz *et al.* (2008) and Carpentier *et al.* (2009). For each life-history stage (except stage 1 and 5 larvae because of their small size

Table I. - Environmental predictors tested during the regression quantile habitat modelling procedure. Maps of each can be found in Carpentier *et al.* (2009). 1: Egg surveys; 2: Larval surveys; 3: Coastal nursery surveys; 4: Larger-scale trawling surveys; *: A measure of the pressure (in Newton per m²) applied on the seabed by tidal currents; **: Five main categories were considered: mud (M), fine sand (FS), coarse sand (CS), gravel (G) and pebble (P); PSU: Practical Salinity Units; UF: Units of Fluorescence.

Environmental predictors	Type	Unit	Survey data modelled	Source
Depth (DEP)	<i>In situ</i>	m	1, 2, 3, 4	Measured during the surveys
Bed shear stress* (STR)	Model	N.m ⁻²	1, 2, 3, 4	Aldridge and Davies (1993)
Seabed sediment type**	<i>In situ</i>	-	1, 2, 3, 4	Larsonneur <i>et al.</i> (1979)
Temperature (TMP)	<i>In situ</i>	°C	1, 2, 3, 4	Measured during the surveys
Salinity (SAL)	<i>In situ</i>	PSU	1, 2, 3, 4	Measured during the surveys
Chlorophyll <i>a</i> (CHL)	<i>In situ</i>	µg.L ⁻¹	1	Measured during the surveys
Fluorescence (FLU)	<i>In situ</i>	UF	2	Measured during the surveys

and gear avoidance behaviour, respectively; see Koubbi *et al.*, 2006), several environmental predictors (Tab. I) were tested for significance contribution through a backward elimination procedure. This started with a full model containing all predictors (first and second order continuous parameters; nominal parameters such as seabed sediment type being introduced as factors) and first order interactions between parameters. The equation of the final model was used within a GIS to recode digital maps of the environmental predictors with the predicted species abundance. Maps of all the environmental predictors can be found in Carpentier *et al.* (2009), and reference to them will be made when interpreting the potential habitat maps. The resulting habitat maps were then standardised to allow for easier comparison amongst results representing different life-history stages or seasons.

For each habitat model, the adjusted coefficient of determination (adj-R^2) was used to measure the proportion of abundance variance explained by the final model. Model performances were also assessed using validation datasets internal to their development, by comparing observed (*i.e.*, survey data) and predicted values of species abundance. First a Spearman's rank correlation coefficient tested for a positive and significant correlation between observed and predicted abundances. Then, a correct classification test checked that the correct proportion (90% in the case of a model at the 90th quantile) of observed values in the validation dataset fell below those predicted (Eastwood *et al.*, 2003). Finally, model (prediction) error, computed as the absolute difference between observed and predicted species abundance relative to the maximum observed value, was mapped to illustrate the prediction performance of the model (the value 1 corresponding to the maximum possible prediction error). Note that the error was set to 0 if the observed value was lower than the predicted value, as it is the expected behaviour of that type of model.

RESULTS

Estimation of length at one year old

The length of one year old dab was estimated to be $L_1 = 6.18$ cm. This value was used to separate data for 0-group and > 1 year old individuals.

Survey spatial distributions

Egg survey

The main high abundance patch of stage 1 eggs (Fig. 3A) was located offshore in the central part of the sampled zone, opposite the Bays of Somme and Authie. A lower abundance patch was detected north of Calais. Kriging error was high where sampling stations were sparser (Fig. 3B).

Coastal nursery surveys

There were two main high abundance patches (Fig. 4A): one around Dungeness on the UK coast and one along the French coast between Boulogne-sur-Mer and the Bay of Somme. Lower abundance patches were found along the north Kent coast, around Beachy Head, and in the Bays of Veys and of Seine. Kriging error was higher offshore where sampling stations were sparser (Fig. 4B).

Larger-scale trawling surveys

The datasets collected in July/August and October partly overlap that of the coastal nursery dataset in that these larger-scale surveys (i) also sampled coastal waters (though at a much coarser spatial resolution) and hence (ii) also caught juvenile individuals. These surveys caught the year's juveniles (0-group maps shown in figure 5) as well as the previous year's juveniles and adults (> 1 year old maps shown in figure 6). Overall, dab spatial patterns, both for age groups considered and for surveys, were coastally distributed.

In July/August (Fig. 5A), 0-group dab showed high abundance patches in the Bays of Seine on the French side and around Dungeness and the north Kent coast on the UK side. There were lower abundance patches along the coast near the Bay of Authie and west of Beachy Head. In October (Fig. 5E), only two high abundance patches were found, one in the Bay of Seine and one east of Dungeness (with lower abundance levels west of there); their surface areas were less than in July/August, contracting towards the coast (note that the north Kent coast was not sampled in October). Again, kriging errors (Fig. 5B, 5F) were higher in the central waters in the western part of the study area and north of Calais, *i.e.*, in areas where sampling stations were sparser and occurrences lower.

In both July/August and October (Fig. 6A, 6E), the spatial distributions of > 1 year old dab were similar to that of younger individuals in July/August: high abundance patches found in the same locations were, however, covering broader surface areas, expanding along the coast and offshore across the eastern English Channel. Lower abundance patches were also detected in the Bay of Veys, in the southern North Sea (July/August) and offshore from Calais (October). Again, the October spatial distributions appeared to contract towards the coasts, when compared to July/August patterns, and the kriging errors (Fig. 6B, 6F) were greater in under-sampled areas and where occurrences were lower.

Modelled potential habitats

The significant predictors of each model are listed in table II, along with the selected quantile, values of adj-R^2 and the results of the model validation tests. Except for one model, all had depth (bathymetry plus mean sea level), bed shear stress and temperature as significant predictors. Fluorescence was a significant predictor (positive relationship for

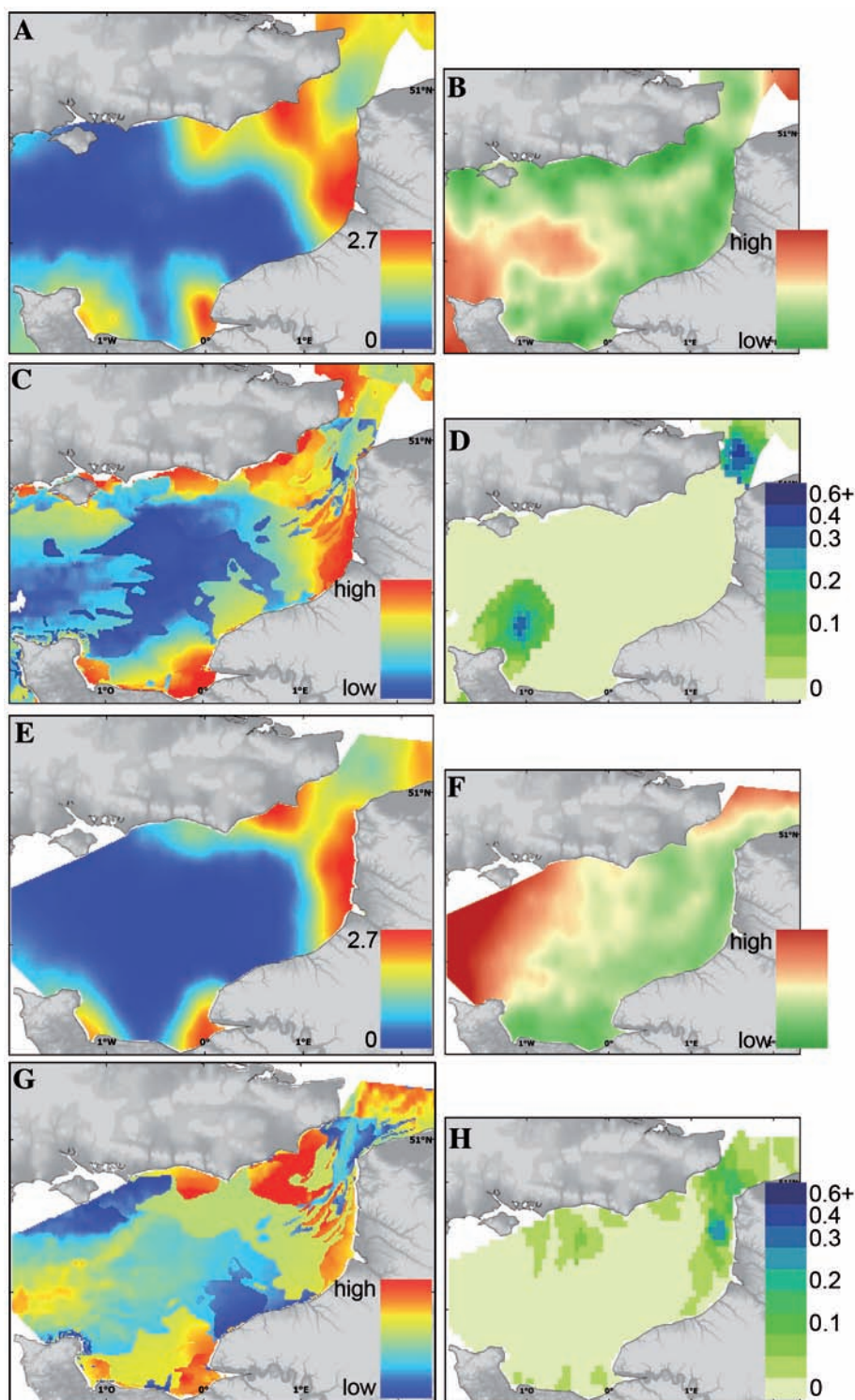


Figure 6. - *Limanda limanda* > 1 year old. **A:** Mean spatial distribution of abundance ($\text{Log}_{10}[x+1]$, $x = \text{nb. ind./km}^2$) in July/August; **B:** Kriging error; **C:** Potential habitat in July/August; **D:** Model error; **E:** Mean spatial distribution of abundance in October; **F:** Kriging error; **G:** Potential habitat in October; **H:** Model error.

all three larval stages) of all three larval stage models, but only one larval model (stage 2) had seabed sediment type

(Fig. 7A, 7C, 7E) covered a significant proportion of the areas surveyed, specifically a large band of shallow to inter-

as a significant predictor whilst all other life-history stages had this predictor in their final model. The predictors with the highest absolute coefficient (i.e., contributing extensively to the final habitat map) varied with the model considered, but it was always either a seabed sediment type, temperature or bed shear stress. All models (except the egg stage) had significant interactions between some of their predictive parameters, and six out of the nine models included second-order polynomial terms; this resulted in complex model equations. The proportion of abundance variance explained by the final model varied between $\text{adj-R}^2 = 0.06$ (coastal juvenile habitat) and 0.53 (> 1 year old in October) and all models passed the Spearman's rank correlation and correct classification tests.

Spawning habitat

The survey patterns (Fig. 3A) were very consistent with the potential habitat (Fig. 3C) except in the northern part of the surveyed area (offshore from Dungeness) where the quality of predicted habitat was more favourable (high predicted abundance levels) than what was recorded during the survey. Model error (Fig. 3D) was low throughout, except for two small areas near to the coast where survey abundance data in the validation dataset were higher than abundance predicted by the model. The January spawning habitat occupied areas of intermediate depth, weak bed shear stress, low Chlorophyll *a* concentration (although in this season, this parameter has very low values throughout, compared to the spring time bloom), and sand and gravel bottoms.

Larval habitat

March/April potential habitats

mediate depths along the French coast where bed shear stress (and tidal currents) are weak to intermediate, temperatures were warmer and fluorescence higher (due to increased seasonal phytoplanktonic activity). The centre of the Dover Strait, where bed shear stress is stronger, was not a suitable habitat (i.e., low predicted abundance levels) for stage 2 larvae (Fig. 7A), but an area offshore from Dungeness and sheltered from strong bed shear stress showed intermediate predicted abundance levels. Stages 2 (Fig. 7A) and 3 (Fig. 7C) larval habitats were located slightly further offshore compared to stage 4 larval habitat (Fig. 7E) for which the warmer shallower coastal waters were most suitable (highest predicted abundance levels) although temperature was not a significant predictor for this stage's model. Stage 4 modelled habitat (Fig. 7E) should be noted with care, however, as few stage 4 individuals were caught during the surveys and the final model has only one significant predictive parameter (fluorescence), despite relatively good model adjustment parameters ($\text{adj-R}^2 = 0.50$ and both validation tests passed). Model errors (Figs. 7B, 7D, 7F) were relatively low, except for stage 2 (Fig. 7B) in offshore waters where survey abundance data (in the validation dataset) were higher than abundance predicted by the model.

Coastal nursery habitat

The coastal nursery habitat (Fig. 4C) was very consistent with survey patterns (Fig. 4A), and the model error (Fig. 4D) was low throughout the area studied, despite the model explaining a small proportion of abundance variance ($\text{adj-R}^2 = 0.06$). Within the coastal band sampled during the surveys, bed shear stress was weak and the waters less saline and starting to cool down, as it is usually the case in September when rain-inflated rivers pour cold freshwater into shallow coastal waters. The September coastal nursery habitat occupied areas with a range of bottom types (mud, sand, pebbles) and where waters were cooler and less saline.

0-group habitat

In July/August, the 0-group potential habitat (Fig. 5C) covered much broader areas than the survey patterns suggested (Fig. 5A), with highly suitable areas being located

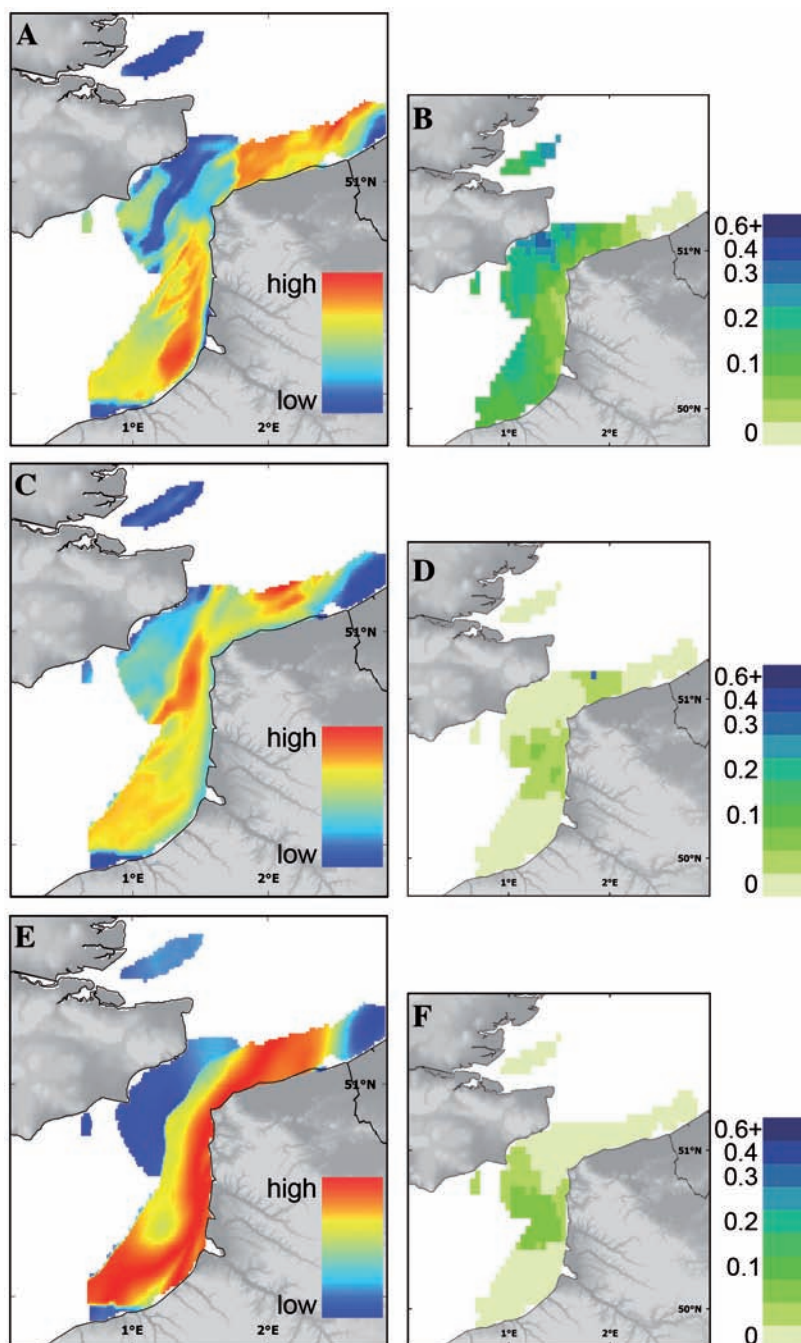


Figure 7. - *Limanda limanda* larvae. Potential habitat in April/May and model error for developmental stages 2 (A and B), 3 (C and D) and 4 (E and F).

along the coasts in all directions on both the French and UK sides. Model error was relatively high (Fig. 5D) north of the Cherbourg Peninsula, indicating that the validation dataset contained abundance values greater than that predicted by the model. Mean abundance levels (Fig. 5A) were however close to zero in this area, but the effect of a few high abundance values (some of which present in the validation dataset) was most likely smoothed out in the mean map. The

Table II. - Significant environmental predictors and adjustment parameters for *Limanda limanda* (regression quantile) habitat models. *: see Table I for abbreviations. + or - indicate that the first order predictor's coefficient was positive or negative. ² indicates that the predictor was present as a second order polynomial in the final model. The seabed sediment types are listed in the order of their coefficient (from the most to least important). Predictors involved in significant interactions are shown in bold (interactions were not tested for the egg stage).

Life-history stage	Selected quantile	Significant predictors*	Adj-R ²	Spearman's rank correlation test	Correct classification test
Eggs	95 th	+DEP ² , -STR, -TMP, -CHL ² , CS/G/FS/P/M	0.20	passed	passed
Stage 2 larvae	85 th	+DEP, -STR ² , +TMP ² , +SAL ² , +FLU ² , CS/G/FS/P	0.41	passed	passed
Stage 3 larvae	85 th	-DEP , +STR, +TMP, +SAL, +FLU	0.40	passed	passed
Stage 4 larvae	90 th	+FLU ²	0.50	passed	passed
Coastal nursery	80 th	+DEP, +STR ² , -TMP ² , -SAL ² , M/P/FS/CS/G	0.06	passed	passed
0-group July/August	95 th	-DEP, -STR , +TMP, M/G/FS/P/CS	0.19	passed	passed
0-group October	85 th	+DEP, -STR , -TMP ² , -SAL ² , FS/G/P/CS/M	-	passed	passed
> 1 year old July/August	95 th	+DEP, -STR² , +TMP ² , -SAL, M/CS/P/FS/G	0.09	passed	passed
> 1 year old October	85 th	-DEP , -STR , +TMP, -SAL, CS/FS/P/M/G	0.53	passed	passed

0-group potential habitat occupied areas of shallow to intermediate depths and tidal currents, exhibiting relatively warm waters (which is the case along the coasts at this time of year) and a range of sediment types (excluding coarse sand).

In October, the potential habitat (Fig. 5G) agrees with the apparent contraction of the autumn survey distribution (Fig. 5E) towards the coast, when compared to July/August survey pattern and habitat. The model also highlighted favourable areas (e.g., Bays of Veys, Somme and Authie, and north of Calais), which were not detected in the survey patterns. Model error (Fig. 5H) was relatively higher in the central waters of the study area, for similar reasons to that explained above. Also, the variance of the model was greater than that of the dataset (adj-R² could not be estimated), meaning that the predictive power of the model was very low. The October habitat occupied coastal areas of shallow to intermediate depths, having weak bed shear stress, fine sediment bottoms and less saline waters starting to cool down (due to discharges from seasonal rain-inflated rivers).

> 1 year old habitat

In both July/August (Fig. 6C) and October (Fig. 6G), the potential habitats were consistent with the survey distributions (Fig. 6A and 6E, respectively), although modelled suitable areas were broader than actual survey patterns, notably along the coastlines but also (only in October, Fig. 6G) in open waters north of the Cherbourg Peninsula. As for the 0-group in July/August, model error was relatively high (Fig. 6D) north of the Cherbourg Peninsula. Also, model errors in July/August (Fig. 6D) and October (Fig. 6H) were higher near to the Dover Strait. In July/August and October, potential habitats were located in areas with shallow to intermediate depths and bed shear stress, soft bottoms (mud and

sand) and where waters were less saline. The October habitat also highlighted as suitable deeper areas showing strong bed shear stress and harder bottoms (pebbles) north of the Cherbourg Peninsula: this should be taken with care, however, as this area is not well sampled during the surveys, as suggested by the high kriging error (Fig. 6F).

DISCUSSION

Spatial patterns from survey data can be understood as a proxy for the "realised habitat" of a species at a given life-history stage (Planque *et al.*, 2007), the realised habitat being the portion of the habitat that was actually occupied by it when the surveys took place. The information these observed patterns bring is valuable (e.g., Mello and Rose, 2005) but, as they are dependent on year-to-year fluctuations, their usefulness in terms of species management is limited. In contrast, habitat modelling is a powerful tool for understanding and interpreting the spatial patterns obtained by interpolating survey data, as habitat models can help explain species response to their environment. Further, geostatistical interpolation may smooth out, for instance, unusually high abundance values encountered during the survey, whilst these would be better taken into account by habitat models.

Spawning habitat

In the eastern English Channel and North Sea, dab is known to spawn its planktonic eggs from March to June (Munk and Nielsen, 2005). It is a batch spawner (Murua and Saborido-Rey, 2003) that releases its eggs as discrete batches over a relatively long period of time. This may account for the presence of dab eggs for a longer period of time (e.g.,

January to August-September, as reported elsewhere, see Daan *et al.*, 1990 and Rijnsdorp *et al.*, 1992) or as early as the end of January (this study's dataset).

Dab spawning grounds have been reported to be offshore, usually at intermediate depth (Henderson, 1998). The present study's results indicated that, at the end of January, dab spawning areas in the eastern English Channel were located in the open sea. This is in line with first quarter commercial landings data presented in the CHARM Atlas (Carpentier *et al.*, 2009; January-March 2000-2004, based on French, UK, Belgian and Dutch fishery logbooks), which also indicated that dab were caught in the central and eastern parts of the area. Despite the coarser spatial resolution of the landings data (by ICES statistical rectangle), commercially exploitable dab appeared to be located further offshore in the first quarter than during the rest of the year. This is consistent with adult dabs being located (most likely to spawn) at the end of January in these areas where eggs were found. The parameters (in terms of sea bed sediment type and bed shear stress) of the potential habitat model for January suggest that areas off the Bay of Somme and Dungeness could be suitable for spawning. However, these coastal waters were not sampled due to vessel size, and data still need to be collected there to further investigate this. The presence of seabed sediment type in the habitat model for a pelagic developmental stage is explained by the fact that eggs are spawned by females at the sea bottom; the eggs then rise until they reach their depth of neutral buoyancy. In the North Sea, January/February (Martin *et al.*, 2007) and March/April (Rijnsdorp *et al.*, 1992) dab spawning areas displayed fine sediment types (mainly sand and gravel), shallow to intermediate depths and weak to intermediate bed shear stress, suggesting that spawning habitats in the eastern English Channel and North Sea are of similar nature.

Larval habitat

Dab eggs hatch after 3 to 12 days of incubation (Russell, 1976) and larval stages remain pelagic until stage 5 individuals metamorphose into demersal juveniles (Rijnsdorp *et al.*, 1995). This study's sampling having taken place in April-May, i.e. during the peak of the spawning season, all five larval developmental stages were present in the samples. As reported in Koubbi *et al.* (2006), young larval stages (stages 2 and 3) were abundant in the central waters of the area surveyed and older ones (stages 4 and 5) were distributed mainly along the French and Belgian coasts. Potential habitats (this study) were consistent with survey patterns and previous habitat modelling attempts (Koubbi *et al.*, 2006).

The movement of dab larvae from offshore spawning areas towards French coastal nurseries is thought to result from dispersal due to the residual current from the English Channel towards the North Sea (Brylinski and Lagadeuc, 1990; Koubbi *et al.*, 2006). This is consistent with this study's habitat models suggesting spatial segregation of

larval developmental stages, with younger larval habitats (stages 2 and 3) being found further offshore than older larval habitat (stage 4, and possibly stage 5), spawning having taken place in the open sea. Unfortunately, the surveys considered here did not sample the UK coastal zone as much as the French one. On the French side, larvae are known to be kept within retention zones that are mainly located off estuaries, in what is termed the "Fleuve côtier", or coastal river (Brylinski and Lagadeuc, 1990; Brunet *et al.*, 1992). This was shown also for sole *Solea solea* (Linnaeus, 1758) and plaice *Pleuronectes platessa* Linnaeus, 1758 (Grioche *et al.*, 1997, 2000, 2001; Koubbi *et al.*, 2006). In March/April, this 3-4 miles wide water mass has higher phytoplanktonic biomass and productivity (and hence abundant prey items for the developing larvae), lower salinity and higher temperatures than offshore waters, from which it is separated by a hydrological front. These coastal areas provide suitable habitat for developing larvae before they metamorphose into demersal juveniles and adopt a highly specialised benthic life-style in nursery areas (Rijnsdorp *et al.*, 1995).

Juveniles and adults

This study's estimation of length at year one ($L_1 = 6.18$ cm) was consistent with that reported by Bolle *et al.* (1994) for dab in the southern North Sea. In that area, bottom-living stages of 0-group dab are found in large numbers in very shallow and sandy coastal waters, but some small 0-group individuals are also found further offshore (Daan *et al.*, 1990). The pattern is consistent with the present study, with results indicating that these young individuals are not only found in coastal areas (as shown by the coastal nursery spatial patterns) but also, to an extent, further away from the coast (0-group spatial patterns). In the eastern English Channel, however, coastal waters shelve more steeply than in the North Sea, which spatially limits the amount of suitable habitat available as a nursery ground for these young stages (Henderson, 1998; Rogers *et al.*, 1998b). In general, the older age groups of the demersal species occur in deeper water than the younger ones (Daan *et al.*, 1990; Riou *et al.*, 2001). This pattern appears to hold true for dab in the eastern English Channel during July/August and October, with 0-group individuals being nearer to the coast in shallow waters, and > 1 year old individuals having broader spatial distributions, notably towards offshore deeper waters.

Seasonal shifts in spatial distributions are known to occur for demersal fish, although migrations are not as remarkable as for some pelagic species (Daan *et al.*, 1990). For instance, > 1 year old individuals were reported across the central southern North Sea in February (Rijnsdorp *et al.*, 1992), whilst they were near to the coast on their feeding grounds in the southeastern North Sea in August-September. Spatial distributions from July/August and October for this age group in the eastern English Channel (the present study) did not

differ much, except for the October distributions being nearer to the coast than the July/August ones. For the 0-group, mortality (high at this developmental stage) could explain the slightly more coastal October distribution pattern, although it could also result from this young stage not being representatively sampled by the GOV trawl used during the October surveys. This was supported by the poor predictive power of the associated 0-group habitat model. Nonetheless, if adults do spawn offshore in January (as suggested by stage 1 egg distribution and habitat model), there might well be a seasonal shift in distribution for dab in this area of the eastern English Channel, with adults being offshore at the start of the spawning season (January) and nearer to the coast on their feeding grounds in July/August and October.

The potential habitat in coastal nurseries was very similar to that of the fish sampled during larger-scale trawling surveys (0-group and > 1 year old individuals). Suitable habitats for these life-history stages were found in areas with shallow to intermediate depths and bed shear stress, low salinity and displaying a range of sediment bottoms (though mainly mud, sand and gravel).

CONCLUSION

The present study has shed light on the spatial distributions and nature of potential habitats of dab *Limanda limanda* in the eastern English Channel. For all life-history stages considered, suitable habitats displayed shallow to intermediate depths and bed shear stress, with the exception of the egg stage habitat (intermediate depth and wear bed shear stress). Except for the two larval stages which did not have seabed sediment type in their final habitat mode, all other modelled habitats depended upon this predictor, although there was a range of suitable bottom types (mainly sand, mud and gravel), depending on the stages and seasons considered. The relationships of dab habitat with temperature (present in all models) and salinity (present in most models) was more variable, again depending on the stages and the seasons. This result is not unexpected as “physical” environmental parameters, such as depth, bed shear stress and seabed sediment type, do not vary throughout the year, at least not on the same scale as “hydrological” ones, such as salinity and temperature.

These results, along with those on 33 other fish species (whose maps are available in the CHARM Atlas), can be used to improve the quality of management and planning advice that is offered to decision-makers in order to elaborate guidelines for the long-term preservation of species and habitats in this (and other) marine area(s). It is for this purpose that the CHARM project (www.ifremer.fr/charm) developed a multi-disciplinary approach in the eastern English Channel. Other areas of the project included an overview of its physical environment (presenting maps of all the

environmental parameters mentioned herein), a review of the legal framework (at national, European and international levels), spatial distributions and modelled habitats of benthic invertebrates, commercial fisheries and fishing communities, a marine spatial planning exercise and a first attempt at developing a trophic network model. Such an integrated ecosystem-based approach to resource management is strongly reliant on first understanding the spatial distribution of ecosystem components such as species and their habitats, so that this knowledge can then be fed into spatial planning and trophic network modelling. The present study, through the concerted analysis of several datasets, has hence demonstrated the potential of the CHARM Atlas to provide the tools and knowledge necessary for a durable exploitation of the resources of this marine ecosystem.

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