

Spatial patterns and GIS habitat modelling of *Solea solea*, *Pleuronectes flesus* and *Limanda limanda* fish larvae in the eastern English Channel during the spring

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SUMMARY: The spring distribution of larval fish stages of flatfishes in the Dover Strait (eastern English Channel) was studied in 1995 and 1999. Fish larvae were identified and sorted according to developmental stages in order to study their ontogenic distribution. The French coastal waters are characterised by an unstable tide-dependent front, which influences larval dispersion. In spring, the French coastal waters have a high phytoplanktonic production. They have higher temperatures, lower salinities and differences in current intensity compared with the central English Channel waters. Generalised Additive Models (GAM) combined with Geographic Information Systems (GIS) were used to model the potential habitats of life stages considering data from three major surveys in this area. The models were developed by coupling presence-absence models with non-null abundance models. The potential habitat of larval stages was then mapped using a geostatistical method (kriging). This revealed different species strategies in which young stages were abundant in central waters and older ones were distributed mainly along the French and Belgian coasts. It is concluded that the central English waters are important for young stages after hatching and that coastal waters are essential nurseries for future juveniles. The models of three flatfish species having similar life cycle strategies are presented here: *Limanda limanda*, *Platichthys flesus* and *Solea solea*.

Keywords: GAM, GIS, Geostatistics, Fish larvae, English Channel.

RESUMEN: PAUTAS DE DISTRIBUCIÓN ESPACIAL Y MODELIZACIÓN MEDIANTE SIG DEL HABITAT DE LARVAS DE *SOLEA SOLEA*, *PLEURONECTES FLESUS* Y *LIMANDA LIMANDA* EN LA PARTE ORIENTAL DEL CANAL DE LA MANCHA DURANTE LA PRIMAVERA. – Durante 1995 y 1999 se estudió la distribución primaveral de los estadios larvarios de peces planos en el Estrecho de Dover (parte oriental del Canal de la Mancha). Las larvas de peces fueron identificadas y separadas en función de su estadio de desarrollo con objeto de estudiar su distribución ontogénica. Las aguas costeras francesas se caracterizan por un frente de marea inestable, que influencia la dispersión larvaria. Durante la primavera, dichas aguas presentan una elevada producción fitoplanctónica. Asimismo, presentan altas temperaturas, bajas salinidades y diferencias en la intensidad de la corriente, comparado con las aguas centrales del Canal de la Mancha. A partir de datos obtenidos en tres amplias campañas en este área, se utilizaron Modelos Aditivos Generalizados (GAM) con Sistemas de Información Geográfica (SIG) para modelizar los hábitats potenciales de los estadios larvarios. Los modelos se desarrollaron uniendo modelos de “presencia-ausencia” con modelos de “abundancia no nula”. A continuación, usando métodos geostatísticos (*kriging*) se representó el mapa del hábitat potencial de los estadios larvarios. Esto reveló diferencias en las estrategias de aquellas especies cuyos primeros estadios son abundantes en las aguas centrales y cuyos estadios más avanzados están distribuidos principalmente a lo largo de la costa francesa y belga. Se mostró la importancia de las aguas centrales del Canal de la Mancha para las larvas lecitotróficas, y como las aguas costeras son áreas de cría esenciales

para los futuros juveniles. Aquí se presentan los modelos para tres especies de peces planos que tienen estrategias de vida similares: *Limanda limanda*, *Platichthys flesus* and *Solea solea*.

Palabras clave: GAM, SIG, Geoestadística, larvas de peces, Canal de la Mancha.

INTRODUCTION

The Dover Strait links the North Sea with the English Channel. Tidal currents and prevailing winds induce a residual circulation from the English Channel to the North Sea. This area is significant for fisheries due to the abundance of fish species as well as the presence of nursery, spawning grounds and migratory routes linked to specific environmental characteristics. Conservation approaches linked to fish-sensitive habitats are thus needed to study the vulnerability of the resource (Carpentier *et al.*, 2005).

Grioche *et al.* (1997a,b, 1999, 2001) showed that the spatial distribution of larval fish stages in the eastern English Channel is related to water masses with variations linked to bathymetry and distance from the coast (thermohaline gradients). Grioche *et al.* (1999) showed that there was a spatial segregation of life stages. For some species, spawning grounds and young stages are offshore in the central eastern English Channel and older stages are found in the coastal waters. Migratory processes can partly counteract the larval drift due to currents, as shown by Grioche *et al.* (1997b, 2000, 2001). Retention zones help fish larvae to remain in a specific area. These zones are linked to oceanographic phenomena, such as fronts and gyres. They are mainly located off estuaries and are linked to the coastal water mass along the Opale Coast, the "Fleuve côtier" (coastal flow), where high temperature, low salinity and high fluorescence (linked to phytoplankton) are observed (Brylinski, 1986; Brylinski and Lagadeuc, 1990). This coastal water mass is separated from central waters by a hydrologic front whose structure depends on tides and meteorological conditions. In spring, the phytoplankton bloom is reinforced along the French coast by high concentrations of *Phaeocystis globosa*.

A species' habitat is related to its real ecological niche as defined by Hutchinson (1957). It is the combination of environmental factors which explains its distribution. In a specific area, the presence of some specimens of a species is due to suitable conditions for its survival. High abundances could be related to optimal environmental condi-

tions, which maintain the population including its growth and reproduction. Fish habitat can be mapped using Geographic Information Systems (GIS) (Koubbi, 2000). Different methods are available for modelling habitats. Linear regressions, first used for habitat modelling, are too restricted because of their statistical requirements and also because a species' response to its environment is not always linear. Habitat suitability index and quantile regressions were also used in fish ecology (Harlay, 2001; Eastwood *et al.*, 2001; Koubbi *et al.*, 2003). In recent years, statistical methods with less restrictive assumptions have been used. Generalised Additive Models (GAM, Hastie and Tibshirani, 1990) are the non-parametric counterparts of Generalised Linear Models (GLM, McCullagh and Nelder, 1989) and were first used in terrestrial ecology to model relations between plants' presence-absence and environmental factors (Yee and Mitchell, 1991). With the development of Geographical Information Systems, GAM and GLM may now be used to map species' habitats. They may be combined with geostatistics in explanatory and predictive studies (Guisan and Zimmerman, 2000) to model biogeographic patterns or species' potential distribution at different scales. Habitat mapping can be used to model environmental scenarios in unknown areas (Koubbi *et al.*, 2003) or to study spatio-temporal changes (Loots *et al.*; pers. information), but it can be also used to summarize spatial patterns from different surveys to map potential optimal habitat, as is presented here.

Some fish populations show a spatial and temporal repartition of life stages following hydrodynamic features (Harden-Jones, 1968). The shift in habitat of each developmental stage—spawning grounds, areas of larval development, nurseries and trophic grounds—indicates that species-environment relationship changes during the life-cycle. In some cases and for some species, these areas can be geographically separated. Mapping potential habitats of larval fish stages provides the opportunity to study how oceanographic features influence fish early life history. This method can combine results from different surveys in a common model which will help to understand what environmental parameters drive spatial repartitions.

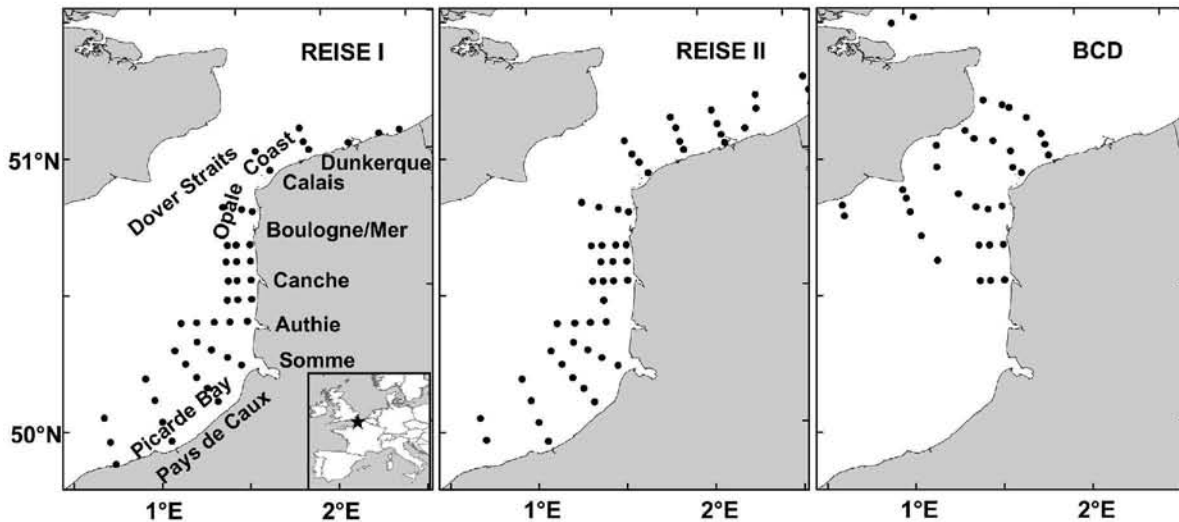


FIG. 1. – Location of sampling stations for the surveys Reise 1 (April 1995), Reise 2 (May 1995) and BCD (April-May 1999). See Table 1.

The larval stages of 3 flatfish species, *Solea solea* (sole), *Pleuronectes flesus* (flounder) and *Limanda limanda* (dab), were studied in order to define their potential habitat, based on spatial ecological models. These species have a similar larval distribution pattern.

MATERIAL AND METHODS

Surveys and database

Data for the years 1995 and 1999 (Fig. 1, Table 1) were chosen because they covered more extensive geographical areas than other survey data available (Koubbi, 2000). In 1995, two surveys of ichthyoplankton were made between the Schelde and Seine estuaries (Grioche *et al.*, 1999). There were 45 stations sampled in April 1995 and 60 in May 1995. Another survey was carried out at the end of April 1999, sampling a total of 39 stations (Koubbi, 2000). The ichthyoplankton was collected with a double-framed bongo gear (63 cm of diameter) fit-

TABLE 1. – Dates of sampling surveys and number of observations. The first two surveys are "REISE" (Répartition de l'écophase ichthyoplanktonique entre l'estuaire de la Seine et de l'Escaut – Ichthyoplanktonic ecophase repartition between the Seine and Schelde estuaries). The last survey is "BCD" (Biodiversity and Cartography of marine resources in the Dover Strait).

Survey	Beginning	End	Number of stations
Reise I	11/04/1995	13/04/1995	45
Reise II	02/05/1995	04/05/1995	60
BCD	27/04/1999	01/05/19,99	39

ted with nets of 500 μm mesh size (Smith and Richardson, 1977). Oblique tows were carried out at a speed of 2 knots from the surface to near the sea bed. The volume of water filtered by each net was measured by means of a flowmeter and was used to calculate larval densities, which were expressed as number of larvae per 100 m^3 .

Sorting and identification of larval stages

All fish larvae were preserved in a 5% formaldehyde seawater solution buffered with sodium tetraborate at sea water pH. The species identification was done according to Russell (1976).

Larval stages were defined by morphological and pigmentation patterns adapted from Ryland (1966) by Grioche *et al.* (2000). Stage 1 represents yolk-sac larvae. Stage 2 represents preflexion larvae, with larvae feeding on prey and no longer on their yolk. Stage 3 is characterised by postflexion larvae and the formation of dorsal and anal fins. In Stage 4 (transition larvae), fins are all formed but the larvae still have their markings. For flatfish, Stage 5 corresponds to eye migration and a metamorphosis. The metamorphosis to juvenile stage follows.

Mapping

ArcGis 8 (Geographic Information Systems from ESRI) and its extensions were used to map data from an Access database. Larval abundances, mean temperature, salinity and fluorescence of the water column came directly from the surveys data, whereas bed shear stress ($\text{N}\cdot\text{m}^{-2}$, resolution of 8 km) and

depth (resolution of 1.8 km²) were post-calculated according to Aldridge and Davies (1993) and Carpentier *et al.* (2005). Depth was the addition of the bathymetry and the mean sea level because it was more relevant than bathymetry alone from an ecological point of view. Environmental and biological data were imported into the GIS as point georeferenced data (latitude, longitude, depth and value) and were then interpolated in raster layer form (based on pixels) using the Geostatistical Analyst extension of ArcGis. Spatial Analyst extension of ArcGis was used to calculate and interpolate the distance of each sample from the nearest coast.

Interpolations were made using geostatistics, which allow a value at unsampled locations to be estimated from sparse sampled data points (Rivoirard *et al.*, 2000). The variogram is a mathematical description of the relationship between the variance of pairs of observations (data points) and the distance separating these observations (h). The variogram is characterised by the range, the sill and the nugget effect, and is calculated among different directions when anisotropy is observed. The variogram model was calculated from each variographic cloud to describe the spatial structure of each parameter. Values at unsampled locations and estimation errors were then calculated by kriging, which takes into account the variogram.

Modelling

The models for developmental stage and for species were established using biological data (larval abundance), environmental factors (mean temperature, salinity and fluorescence of the water column, mean depth) from surveys, and other factors such as the distance from the nearest coast or the bed shear stress. Stage 1 samples (yolk sac larvae) were not included in the models because they are not well caught in this period and also because of their small size. Stage 5 samples were also not included because they were not correctly caught by bongo nets either because they avoided the nets or because they were more suprabenthic stages (Grioche *et al.*, 2001).

The Generalised Additive Model (GAM) is a non-parametric method for determining the shape of the response curves from the data, instead of fitting an *a priori* parametric model. It is data-driven rather than model-driven. The response of the species to each predictor (environmental factors) was modelled in a smoothing way. Smoothed responses were

then added to obtain a global response, forming an Additive Model. The response can be presence-absence or abundance data. As there was an overdispersion of abundance data linked to the high number of null data and dispersion indexes greater than 1 (Southwood and Henderson, 2000), the method of Welsh *et al.* (1996) was applied. Data were first encoded in terms of presence-absence for which a model was calculated, then zeroes were eliminated and abundances were modelled. Binomial distribution and logit link for presence-absence data and Poisson distribution and log link for non-null abundances were used (Hastie and Tibshirani, 1995; Southwood and Henderson, 2000; Quinn et Keough, 2002). A smoothing function, i.e. loess or spline types, was then applied separately on each environmental variable. The number of predictors to keep, the choice of the smoothing function and the fit of the models were determined using the deviance, which represents the difference between predicted and observed data. A stepwise selection of the environmental variables was achieved. First, a global model including all predictors was calculated. From this model, several reduced models were tested by withdrawing one predictor (environmental variable). Deviances for all models were calculated and predictors were classified in order of importance and tested towards the global model using an F test on deviance. A probability greater than 0.05 meant that there was no significant differences between the two deviances tested. From the reduced model, we then eliminated the second least important predictor by testing deviance. The procedure was applied until the minimum number of predictors for calculating a model was reached. The model with the fewest environmental factors was kept when two models were equivalent. For each developmental stage and species, two models were computed: one for presence-absence and one for non-null abundance values. The models were performed with S+ software.

As GAM does not produce an equation that can be easily input into GIS, the method described by Lehman (1998) was used to map results at unsampled locations. Models were applied on a regular grid resulting from the resampling of each environmental map by GIS. For each survey and for each point of this grid, a predicted value of presence was obtained (which is a probability of presence) as well as a predicted value of abundance. These two values were multiplied (Welsh *et al.*, 1996; Barry and Welsh, 2002), resulting in a predicted value of

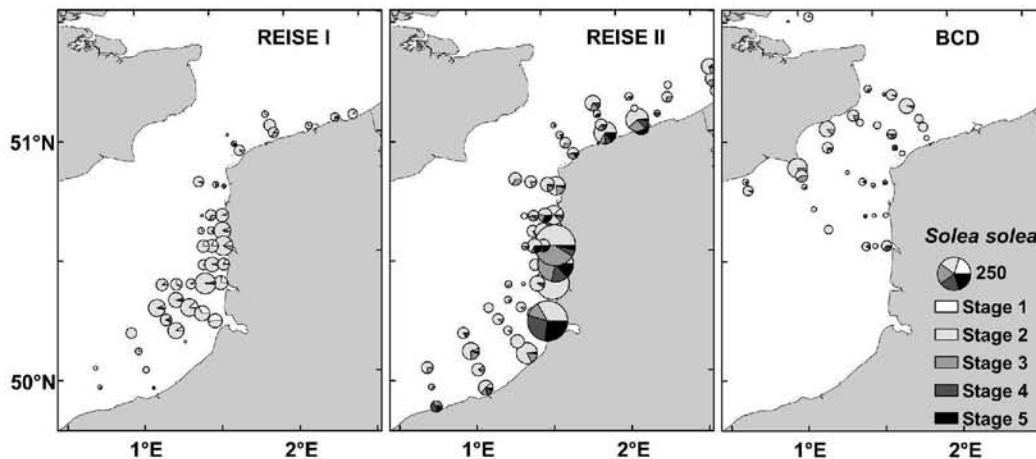


FIG. 2. – *Solea solea* (sole) larval developmental stages abundances for the surveys Reize I (April 1995), Reize 2 (May 1995) and BCD (April-May 1999). Number of larvae/100 m³.

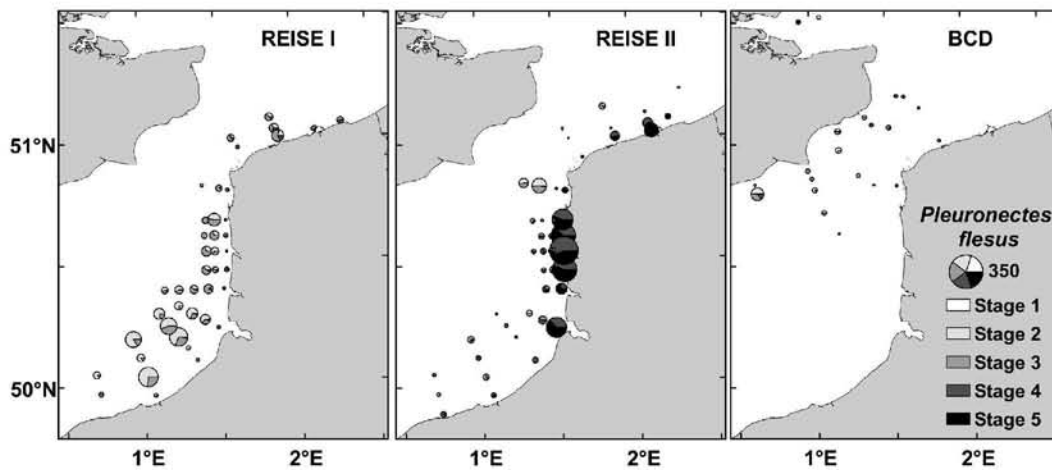


FIG. 3. – *Pleuronectes flesus* (flounder) larval developmental stages abundances for the surveys Reize I (April 1995), Reize 2 (May 1995) and BCD (April-May 1999). Number of larvae/100 m³.

abundance that took into account the presence-absence probability. The models were only applied to the environmental ranges that were used to create them to avoid the risk of extrapolation. To map, the highest value of each point (there was one point per survey, hence a maximum of three) was kept and the grid was interpolated using geostatistics and kriging.

RESULTS

Sole larvae were caught in each survey (Fig. 2). Stages 2 and 3 were mainly found in offshore waters along the French coast and near the English coast. Older stages (stages 4 and 5) were observed mainly along the French coast in May 1995 and were abundant from the bay of Somme to the bay of Canche and along the northern French coasts.

Flounder larvae were only caught in April and May 1995 (Fig. 3). Spatial segregation of larval stages shows that the young larvae (stage 2 and 3) were mainly located in offshore waters whereas larvae of stage 4 and 5 were located closer to the coast, mainly along the Opale coast from the Bay of Somme to the Straits. A second group of larvae was also abundant along the northern coast of France.

Dab abundances show that in April 1995 few young larvae were caught (Fig. 4). They were mainly stage 2 larvae located in offshore waters of the Picarde Bay at the latitude of the Bay of Somme. In May 1995, abundances were the highest of the three surveys. Larvae of stage 3, 4 and 5 were mainly observed from the bay of Authie to the Straits, and the older ones (stages 4 and 5) more along the Opale Coast in coastal waters. In April-May 1999, very few larvae were caught and only offshore in the central part of the Straits.

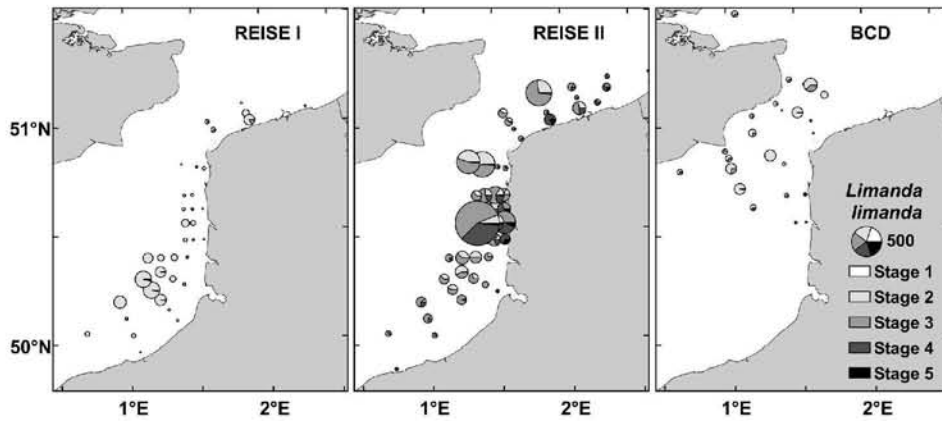


FIG. 4. – *Limanda limanda* (dab) larval developmental stages abundances for the surveys Reise 1 (April 1995), Reise 2 (May 1995) and BCD (April-May 1999). Number of larvae/100 m³.

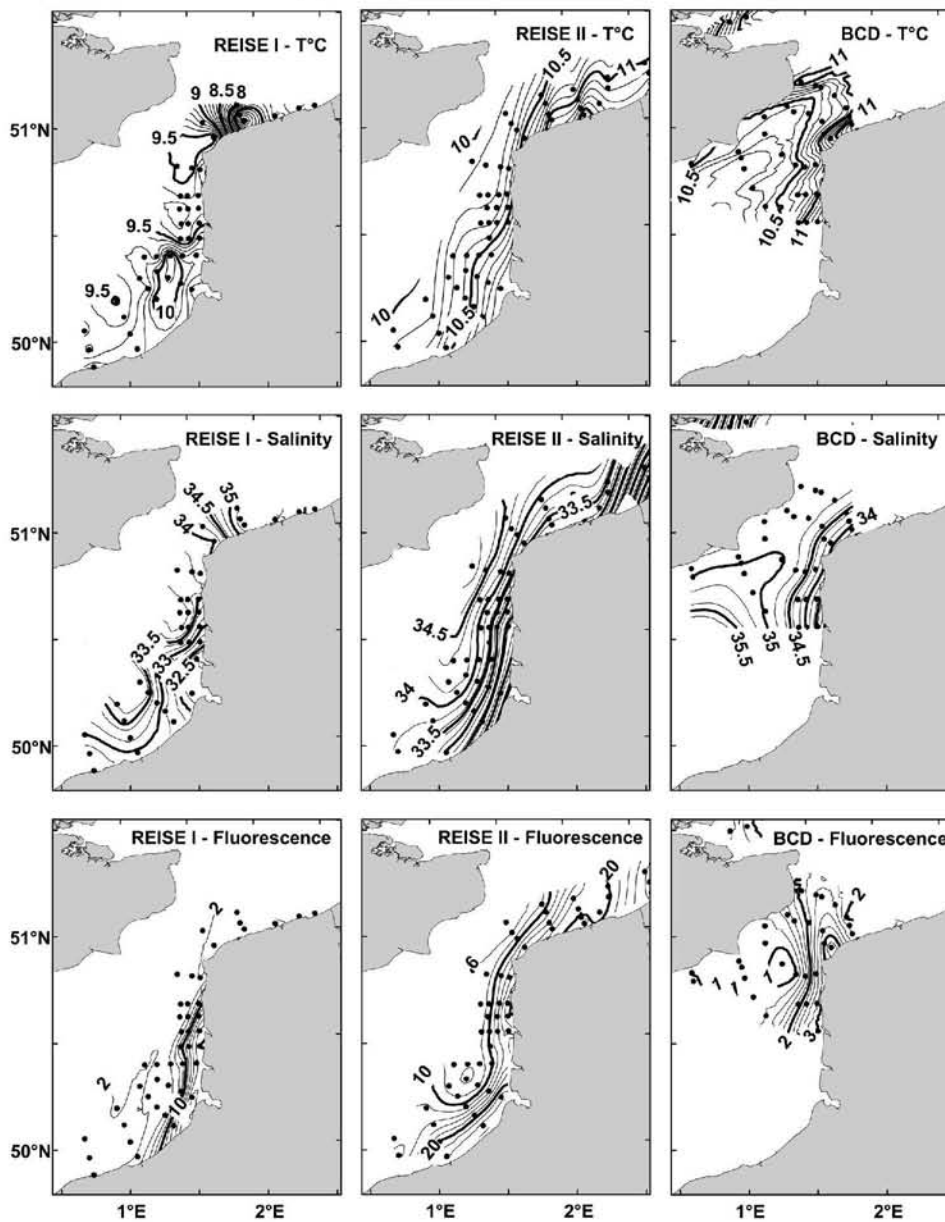


FIG. 5. – Distribution of mean vertical Temperature (°C), Salinity (psu) and Fluorescence (volts) for the surveys Reise 1 (April 1995), Reise 2 (May 1995) and BCD (April-May 1999).

TABLE 2. – Mean and standard deviation (sd) of mean vertical Temperature, Salinity and Fluorescence for each survey.

Survey	Temperature (°C)		Salinity (psu)		Fluorescence (volts)	
	mean	sd	mean	sd	mean	sd
ReiseI	9.36	0.77	33.53	0.93	5.12	6.87
ReiseII	10.56	0.49	33.27	1.25	14.77	9.43
BCD	10.78	0.45	34.57	0.49	1.92	1.26

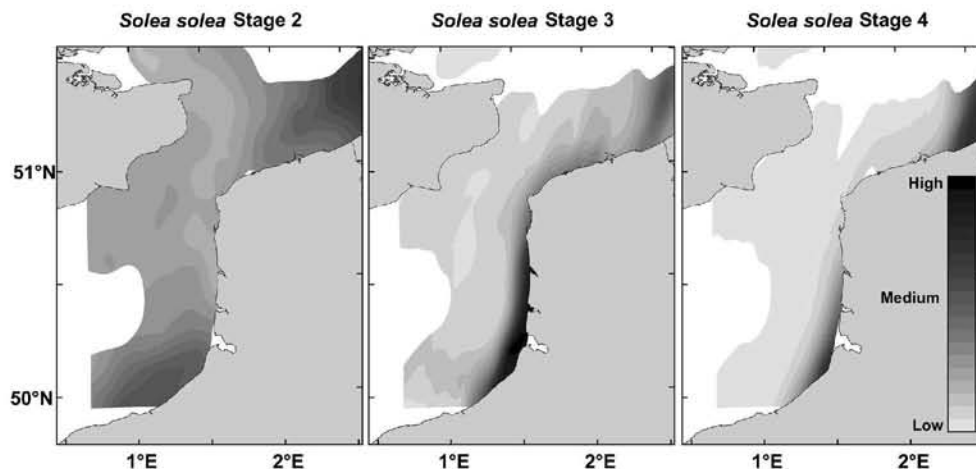
The maps showing environmental factors are given in Figure 5 for mean vertical temperature, salinity and fluorescence and the statistical characteristics are given in Table 2. Differences were observed between surveys. In 1995, the French coastal waters South of the Dover Straits were clearly separated from central English Channel waters. These differences were less great in April-May 1999, except in the Thames estuary and north of the

Straits, where the temperatures were particularly high. The April-May 1999 survey showed very low fluorescence. The hydrological parameters showed three different zones: a water mass going from the central eastern English Channel to the southern bight of the North Sea, which had an Atlantic origin (salinities >34.5); coastal zones showing a coast-to-offshore gradient which was particularly high along the French Coast, where lower salinities (<33.5) and higher temperature and fluorescences were observed; and finally the Thames estuary with low salinities and high temperatures.

The environmental parameters kept in each model according to the stepwise selection are given in Table 3. Raster maps of larval stage distribution obtained from habitat modelling are given in Figures 6 to 8. Optimal habitats derived from the three surveys were standardised for each developmental stage.

TABLE 3. – Parameters of the habitat suitability model and environmental parameters used in it (x). Abundances are for non-null abundances.

Species	Stage	Data type	Smoothing function	Depth	Distance to coast	Temperature	Salinity	Fluorescence	Shearbed stress
Dab	2	Presence absence	loess	X	X	X	X	X	X
	2	Abundances	spline	X	X				
	3	Presence absence	loess	X		X	X	X	X
	3	Abundances	loess	X		X	X	X	X
	4	Presence absence	spline	X		X		X	
	4	Abundances	spline	X		X	X	X	
Flounder	2	Presence absence	loess	X	X	X	X	X	
	2	Abundances	loess		X	X		X	X
	3	Presence absence	loess	X	X	X	X	X	X
	3	Abundances	loess	X	X	X		X	
	4	Presence absence	spline			X		X	
	4	Abundances	spline	X	X	X		X	X
Sole	2	Presence absence	loess	X	X	X	X	X	X
	2	Abundances	spline	X	X		X	X	X
	3	Presence absence	spline	X			X	X	
	3	Abundances	spline		X	X	X	X	
	4	Presence absence	spline	X		X		X	
	4	Abundances	spline	X			X	X	X

FIG. 6. – Suitable habitat, as resulted from the GAM model, for *Solea solea* (sole) larval developmental stages in the Dover strait in Spring.

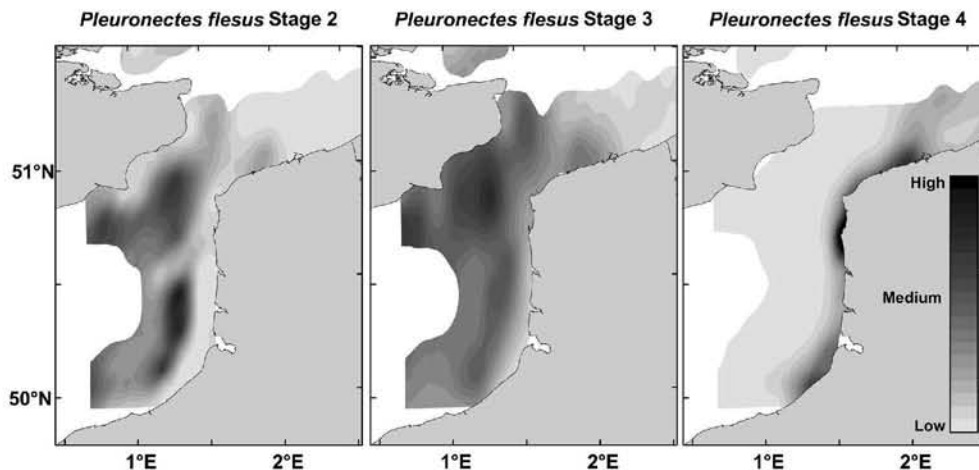


FIG. 7. – Suitable habitat, as resulted from the GAM model, for *Pleuronectes flesus* (flounder) larval developmental stages in the Dover strait in Spring.

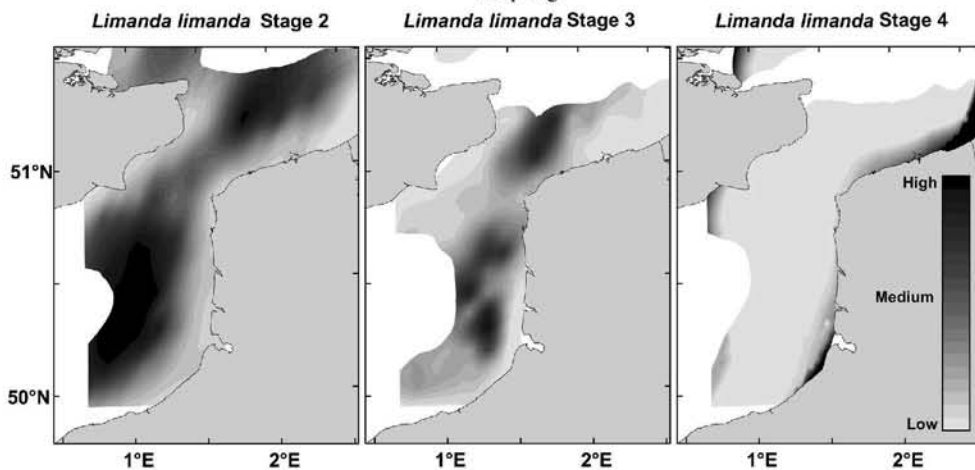


FIG. 8. – Suitable habitat, as resulted from the GAM model, for *Limanda limanda* (dab) larval developmental stages in the Dover strait in Spring.

For sole, all environmental factors seemed to be important in defining the stage 2 habitat, whereas for older stages a combination of fewer factors was found. Depth, salinity and fluorescence were the most common factors included in the models. The potential habitat for stage 2 larvae was along the Flanders coasts and near the Pays de Caux, in the central zone of the English Channel (Fig. 6). Older larvae had a more coastal preferential habitat, which can be explained by a retention phenomenon linked to estuaries.

Temperature, fluorescence, distance from the coast and depth were the most common factors used to calculate flounder larvae habitat. Salinity linked to central English Channel waters was important for determining the presence of stages 2 and 3. Young stages of flounder larvae had a preferred habitat in the central waters of the Channel and along the English coast. Developmental stage 4 was found along the French coast, where waters are warmer with high fluorescence.

All environmental factors were important for determining the presence of Dab stage 2 larvae, but only depth and distance from the coast were relevant for modelling abundances. A combination of depth, temperature and fluorescence mainly defines the habitat of the other stages. The dab larval habitat was found offshore in the whole area for stages 2 and 3. Stage 4 was scarce and limited to the very coastal zone.

DISCUSSION

Habitat modelling

Direct surveys of species distribution and abundance study a small proportion of an area. Sampling stations are scattered in space and time, meaning that they are insufficient to understand and monitor species distribution on a fine scale. Each survey is a

snapshot of the relation between species and environmental factors because of temporal and spatial variability. A survey is linked to local particularities such as weather or timing of planktonic blooms which influence, for example, larval distribution and abundance. Geographic gaps in species distribution can also create difficulties in conservation issues when critical habitats have to be mapped, such as the ones of young stages of fish. Consequently, a map of a survey is not a map of potential habitats.

Habitat modelling provides a means of dealing with information gaps in survey results. It can also be used to test environmental scenarios in species habitats and is a tool for modelling species distribution in unknown areas where environmental factors are known (Koubbi *et al.*, 1993). The resolution of habitat maps will depend on the resolution of environmental factors, as we know that spatial variability is better modelled for abiotic factors than for species abundances because of patchiness and sampling errors. The models are here used to gather information from different surveys to map optimal habitats during the season according to presence and maximal modelled abundances.

Habitat modelling deals with complex species responses to multiple interacting factors. In representing these responses, there is a danger of generating simple models that cannot deal with the complexity of species-habitat relationship. Most ecologists accept that species have a bell-shaped response to environmental gradients. A bell-shaped curve response is hardly ever found because of the high number of null-abundances that indicates a patchy distribution of species. Patchiness for fish larvae depends on the scale of observation. At a small scale, it is linked to the schooling behaviour of the larvae. At mesoscale, it indicates the influence of hydrological features such as fronts and retention zones, which is what is modelled through GIS. Habitat modelling complexity can be related to what Scott (1992) pointed out: we have to cope with data that can be non-normal, multimodal or asymmetric. If different developmental stages have different models it means that their relation with the environment evolves while they are growing.

GAM on presence-absence and non-null abundances offers an interesting alternative approach to solve most of the problems dealing with habitat modelling. Response curves are better estimated and less influenced by the high number of null-abundances. Between presence-absence and non-null

abundances models, the factors kept are not always the same. Multiplying and combining them gives us the optimal habitat of each stage and shows the factors that are important for the presence and the best conditions (areas associated with high abundances).

Life stage distribution

The three studied species showed the highest abundances along the coastal zone from the Somme estuary to Boulogne-sur-mer, and exhibited spatial segregation between their spawning grounds offshore (estimated from the distribution areas of larval stages 2 and 3) and their coastal nursery areas (where older larvae were found, stages 4 and 5).

Sole larvae appeared to be relatively ubiquitous in terms of environmental development conditions. High larval sole abundance and the estimated optimum habitat were near the French and Belgian coast on sand areas of the coastal zone. The straits where high shear bed-stress is observed seemed to be avoided. The optimal habitat of these stages is mainly located in the southern part of the study area near Pays de Caux and in the North Sea along the French and Belgian Coasts. These habitats are located close to known spawning grounds for this species and are in accordance with the egg and larval stage distribution described by Grioche *et al.* (2001) and Eastwood *et al.* (2001). This may be linked to the strategy of having the youngest larvae in areas with lower currents, which allows their retention and spawning in shallow waters with high temperatures and fluorescence (Grioche *et al.*, 2001). Larval stages 3 and 4 show a more coastal distribution associated with the lowest salinity and warmest water, which is in accordance with mapping of survey data from Grioche *et al.* (2001). In the eastern English Channel these larvae show tidal and diel vertical migrations, even for the youngest stages (Grioche *et al.*, 2000). This behaviour favours transport during ebb and limits the advection of this species to the North Sea, which might explain why larvae and juveniles are spatially close together (Grioche *et al.*, 2001; Eastwood *et al.*, 2001; Carpentier *et al.*, 2005).

Spatial segregation of flounder larval stage habitat is shown for this area and is in accordance with survey results described by Grioche *et al.* (1997b). Flounder larvae must reach estuaries, where their nurseries are located. Two phases are identified during larval development. The first phase is one of dis-

persion and advection of young developmental stages towards the coast; these larvae then remain trapped off the coastal frontal zone in areas of greater depth, colder waters and higher salinities. Flounder larvae begin vertical migrations at the stage of notochord flexion (stage 3) when they reach coastal waters, as shown in our models and survey observations (Grioche *et al.*, 1997b). Stage 4 larvae are located in the coastal water mass mainly along the eastern part of the eastern English Channel, where high temperatures and fluorescence are observed. This second phase is one of active migration for older stages, helped by fins, and probably of clear vertical migrations: older stages reach the bottom of the water column, especially during ebb which favours their transport to the coast, as found by Grioche *et al.* (2001). This transport is also enhanced during spring tide, when large displacements bring offshore water close to the shore (Grioche *et al.*, 2000). Their movement against the residual current would appear to be significant so they can reach coastal waters. Juveniles aggregate in estuaries.

Dab spawning grounds are in waters from 20 to 40 m deep (Rijnsdorp *et al.*, 1992), a depth range corresponding to the waters of the central English Channel where pre- and postflexion larvae occur. Among the three species, dab larvae have the largest spatial extent in the area. Optimal larval stage habitats show that the habitat is wider for stage 3 than stage 2, showing a drift to the North Sea and towards the coast. Stage 4 larvae were scarce during April and May, and their habitat was difficult to model because of the lack of data. However, this stage seemed more coastal and its most suitable habitat was along the coast of Belgium. The habitat of these larvae must be studied with surveys on the nearshore zone, where transition larvae and juveniles might occur as they reach sandy beaches (Rijnsdorp *et al.*, 1995).

Harden-Jones (1968) showed how fish spatial distribution during their development can be superimposed on oceanographic features. For some species, spawning grounds, nurseries and adults are geographically separated in function of the currents. The three species have the same migratory pattern, with slight variations between them that can be explained by hydrodynamic features. We show the excellent coupling between flatfish life-cycle strategy and spatial distribution of larval stages. Sole has more defined spawning grounds than the two other species for which young larvae occur almost every-

where. There is a dispersal factor of larvae between the spawning grounds and nurseries resulting from the residual current from the English Channel to the North Sea under usual wind conditions. Along the French coast, the residual current is also to the north, but with a lower intensity. Larvae will either reach the North Sea, especially the Belgian sandbanks, quite rapidly or cross the French coastal frontal zone (Grioche and Kouubi, 1997). The coastal nurseries of older larvae and juveniles (Carpentier *et al.*, 1995) are often associated with retention processes (gyres or frontal zones), which are necessary for survival and growth. This apparently optimal habitat might be linked to optimal foraging conditions and more hydrological stability. These areas are either in river plumes or along the French coastal zone where they are limited offshore by a front. Along the French coast, these waters show higher temperatures and a high level of fluorescence linked to *Phaeocystis globosa* bloom in spring. Finally, these retention structures need to be temporarily destroyed to allow immigration and emigration of individuals but also to regenerate plankton production, especially during the bloom, which can be a problem for secondary production. To complete this displacement from spawning grounds to coastal nurseries, Grioche *et al.* (2000) showed that the vertical behaviour of fish larvae is also important in order to understand how they can remain in an area of high current or choose their directions.

At the present time, it is not possible to estimate the proportion of larvae remaining in the English Channel or mixing with those from the North Sea spawning grounds. Habitat modelling is related to metapopulation theories. One or more populations of many species can occupy patches of optimal habitat, moving from one to another either by migration or advection processes. These species exist in a number of populations that are either isolated from one another or have exchanges of individuals, which is probably the case for the eastern English Channel and southern bight of the North Sea.

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