

Relative contributions of different sole and plaice nurseries to the adult population in the Eastern Channel: application of a combined method using generalized linear models and a geographic information system

Philippe Riou^a, Olivier Le Pape^{b*}, Stuart I. Rogers^c

^a *Laboratoire DRV–RH, station de Port-en-Bessin, Ifremer, avenue du G^{al} De Gaulle, 14520 Port-en-Bessin, France*

^b *Laboratoire Écohal, Ifremer, rue de l'île d'Yeu, BP 21105, 44311 Nantes cedex 3, France*

^c *Lowestoft Laboratory, CEFAS, Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK*

Received 10 April 2000; accepted 1 February 2001

Abstract – The Eastern Channel (ICES division 7d) is considered a unit for stock management of the common sole *Solea solea* and the plaice *Pleuronectes platessa*. At this scale, the aim of this work is to model the juvenile distribution of these flatfish. The database used, based on different surveys undertaken during the two last decades, includes 4500 coastal beam trawl hauls throughout the Eastern Channel coasts. Multivariate analyses are used to study the interannual fluctuations in flatfish recruitment of the region. This approach allows us to separate the Eastern Channel into homogeneous sectors with regard to these fluctuations. The physical parameters that contribute to the observed juvenile sole and plaice distributions are identified and their distributions are modelled using generalized linear models. The results of these models, and the areas of the different populations derived from a geographic information system, are used to identify the main nursery grounds and to compare their respective importance. This quantitative approach identifies the lack of estuarine dependence of the nursery grounds, and highlights those areas where anthropogenic disturbance could influence these populations. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

statistical models / geographical information system / nursery grounds / *Pleuronectes platessa* / *Solea solea* / Eastern Channel

Résumé – Contribution respective de différentes nourriceries côtières aux populations adultes de sole et de plie: étude par couplage de modèles linéaires généralisés avec un système d'information géographique. Ce travail a pour objectif de modéliser la répartition des juvéniles de sole *Solea solea* et de plie *Pleuronectes platessa* à l'échelle de la Manche Est, unité de gestion des stocks halieutiques (division CIEM 7d) pour ces deux espèces. Pour ce faire, l'ensemble des données recueillies le long des côtes de la Manche Est de 1978 à 1998 lors de campagnes scientifiques menées avec un chalut à perche (4 500 traits de chalut) a été collecté. Des analyses multivariées ont tout d'abord permis d'étudier les variations spatio-temporelles de répartition de ces juvéniles et de découper la Manche Est en différents secteurs côtiers homogènes au regard de ces fluctuations. Puis, les paramètres physiques qui conditionnent cette répartition (bathymétrie, structure sédimentaire) ont été utilisés afin de décrire les densités de juvéniles à l'aide d'un modèle linéaire généralisé. Les résultats de ce modèle ont enfin été couplés avec un système d'information géographique afin d'identifier les secteurs de nourricerie de poissons plats. Cette approche a permis de mettre en évidence la spécificité de la Manche Est au regard de ces répartitions et d'identifier les principaux sites côtiers sensibles du fait de leur fonction de nourricerie. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

modèles statistiques / système d'information géographique / nourricerie / *Pleuronectes platessa* / *Solea solea* / Manche Est

1. INTRODUCTION

Coastal zone systems are highly productive areas and act as nursery grounds for many marine species of

commercial importance (Costanza et al., 1997). The constant demands on the coastal zone from a wide range of human activities suggest that the continued function of the natural communities in some areas may

*Correspondence and reprints.

E-mail address: olepape@ifremer.fr (O. Le Pape).

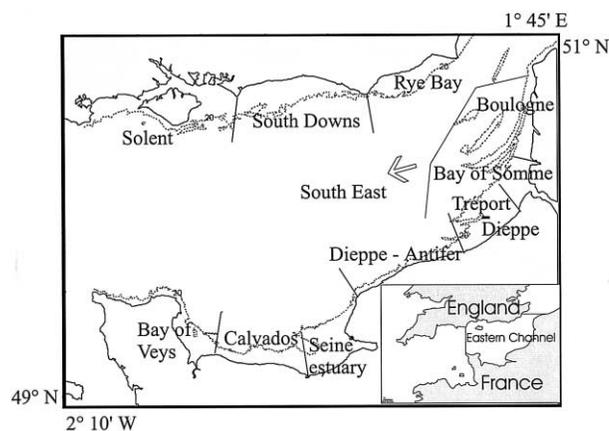


Figure 1. Eastern Channel location with the position of the coastal sectors used in this analysis.

be under threat. The most environmentally sensitive coastal areas will be those where the majority of a resource (such as flatfish nursery areas) is restricted to a few sites (Parrish et al., 1997).

The inshore waters of the Eastern Channel (ICES Division 7D; *figure 1*), a shallow (generally less than 40 m) area, support nursery areas for several commercially important species. The objective of this paper is to identify and describe the coastal nursery grounds of the Eastern Channel for sole *Solea solea* and plaice *Pleuronectes platessa*, the main flatfish landed in the Eastern Channel (respectively 4400 and 7100 t·year⁻¹ on average between 1986 and 1997; anonymous, 1999).

The analysis is based on a number of surveys for juvenile flatfish species, undertaken throughout the Eastern Channel during the two last decades and representing 4400 beam trawl hauls. Using multivariate analysis, generalized linear models (GLM), and a geographic information system (GIS), key sites of importance to the early life-history stages of these commercial stocks are identified and described.

Table I. Summary of the beam trawl data used in this analysis*.

Zone	Period	Number of hauls	Trawl width (m)	Number of chains	Mesh (mm)
English Coast	1980–1998	200 per year	2	3	6
French Coast	1977–1983	75 per year	4.5	2	25
Bay of Somme	1979–1998	80 per year; spring: 250	2	1	20
			3	1	20
			3	0	20
Seine Estuary	1981 and 1995–1998	50 per year; spring: 130, winter: 110	2	1	20
			3	1	20
			3	0	20
Bay of Veys	1978–1981	25 per year; spring: 160	3	2	20
			4.5	1	25

* All surveys were conducted in September and October unless shown otherwise. Surveys in spring and winter show the respective number of hauls in these surveys. Further details of survey methodology can be found in Rogers and Millner (1996) for the English Coast, Mesnil (1983) for the French Coast, Halgand et al. (1998) for the Bay of Somme, Morin et al. (1997) for the Seine Estuary and Beillois et al. (1979) for the Bay of Veys.

2. MATERIAL AND METHODS

2.1. Problem of studying young fish

One of the main problems with the study of juvenile sole and plaice is related to the catchability of very small (0-group) individuals, known to live in shallow intertidal areas where it is not always possible to fish (Riley et al., 1981; Rogers and Millner, 1996, Morin et al., 1997). Because of the difficulties of accurately sampling juvenile flatfish over such a large geographic area, this study is based only on the catch rates of 1-group juvenile flatfish. Dorel et al. (1997) and Hanson (1996) demonstrate that these 1-group fish live in deeper water than 0-groups, where fishing surveys are easier to operate and provide more consistent results between regions and countries. For the species studied, the 2-group fish, living in even deeper areas, are generally not concentrated on nursery grounds (Anonymous, 1993) and are therefore not taken into account.

Hence, the distribution of these 1-group populations is used to describe the seaward limit of the nursery grounds. It is acknowledged that on the landward side the distribution of the nursery ground reaches the inter-tidal zone, where 0-groups are most abundant.

2.2. Beam trawl survey data

For the two last decades in the Eastern Channel, a number of independent beam trawl surveys for juvenile flatfish species have been undertaken throughout the Eastern Channel coastal zone (*table I*). All of these surveys have been collated for this study of the flatfish nursery grounds, this database including 4 400 coastal beam trawl hauls.

These beam trawl surveys use a range of gear types (*table I*) and before analysing these data, it has first been necessary to transform them to intercalibrated values. The main parameters that influence the catchability of beam trawls for juvenile flatfish are the width of the beam, the number of tickler chains and the mesh

size (Fanning, 1994). Previous analyses transformed the catch data into a single unit (number \times m⁻²). For the gears studied (*table 1*), experiments have demonstrated that catches of 1-group flatfish are not affected by the width of the beam trawl, and do not require selectivity corrections within the range of beam trawl mesh size used (Le Pape et al., 2000, and Riou, 1999). The single correction concerns the number of tickler chains, for which correction coefficients according to the sediment structure (Kuipers, 1975; Creutzberg et al., 1987; Dorel et al. 1985 and Dorel, unpublished data) are used (Le Pape et al., 2000, and Riou, 1999).

For these trawl hauls, data describing bathymetry (in meters) and sediment structure are available. Bathymetry is determined from charts according to the position of the haul, and granulometry of the sediment at each station is categorized in three classes: fine sand (including mud, sandy mud and muddy sand), sand and all coarser sediments. It is not possible to categorize the granulometry into more classes, as these three classes were the single common distinction between the hauls on the English Coast, for which granulometry is estimated for each haul (Rogers and Millner, 1996) and these on the French Coast for which granulometry is taken from the map of Larsonneur et al. (1982).

2.3. Quantitative data analyses

In order to study the juvenile distribution, the following quantitative methods have been used:

- First the seasonal variations of flatfish juvenile distributions have been studied: analysis of these fluctuations has been undertaken for French data for all years (*table 1*) when surveys are available for different seasons. Bay of Somme, Bay of Veys and Seine Estuary data were used for the comparison between autumn and spring, and Seine Estuary only for the comparison between autumn and winter. Average densities are computed according to bathymetry, pooled in eight classes every 4 m in order to obtain enough data in each class and, hence, smoothed data (all of the available years are pooled). These data are used to calculate the cumulative frequencies from these averages per class and the study is based on these frequencies.

Hence, to study the interannual fluctuations in juvenile distribution, two different types of factorial analyses are used, the multiple factorial analysis (MFA) and the multiple correspondence analysis (MCA).

A MFA is a principal component analysis using groups of variables (multi-table analysis). Separate variables are identified as columns in a table, and several tables (or groups of variables) are constructed. Each group of variables has the same weight in the calculation of the distances of inertia (Escoufier and Pagès, 1994). This method is especially useful to include several years in a single analysis for a multivariate factorial analysis (each year is a table of the multi-table analysis). In order to analyse the survey

data according to MFA, only those hauls performed every year at the same geographic position (called 'trawling stations') are considered. The data set is studied with a MFA undertaken using the trawling stations as observations (or rows), the log-transformed sole and plaice densities $\ln(x + 1)$ as variables (or columns), and the years as groups of variables. It is hence necessary to work only on a part of the data for which the same trawling stations are visited for the same years. It is the reason why, to include a significant number of years and trawling stations in the analysis, trawling stations from two different surveys, the Bay of Somme and a portion of the English Coast, are combined (*table 1*). This MFA is used to study the interannual variation of juvenile densities between these different sectors.

A MCA is a multivariate factorial analysis based on some semi-quantitative variables. It is sometimes preferred to a principal component analysis on fish ecology because, even if they are log-transformed, fish density values have a very heterogeneous distribution and a low number of values represents the main part of the total inertia and influences the result. Hence, to analyse thoroughly the interannual fluctuations of juvenile distributions between nursery sectors, MCA were undertaken on juvenile densities, divided into three classes (low, medium and high).

If the MFA has been led on the juvenile densities per trawl hauls, the high proportion of zero values, 73% for both 1-group sole and plaice, leads to difficulties in the application of statistical analyses. It is the reason why, in the MFA and the other statistical analyses used in this study, it was useful to pool the data to obtain more statistically valid distributions. Such a transformation is frequently used in fishery science for survey data (Porch and Scott, 1994 and Porch, 1995). The data have hence been pooled according to probability criteria: the presence-absence nature of these data can be considered as binomial, with a probability of 0.73 for the absence of fish. If we consider that the number of zero values has to be less than 5% to work on statistically exploitable data, the number of hauls to be pooled is the minimum value of the first parameter n (number of hauls) of a binomial law $B(n,p)$ for which the associated probability is less than 5%: $p(B(n, p)) < 0.05$ with $B(n,p)$: binomial law with a probability $P = 0.73$. That means the minimum value of n for $(0.73)^n < 0.05$ so $n = 10$. Hence, to analyse thoroughly the variation of the juvenile densities between different nursery sectors, an MCA was undertaken on strata, for which at least 10 trawl hauls are available as individuals, and the 1-group sole and plaice semi-quantitative pooled densities as variables.

The aim of the work was therefore to obtain a global quantitative description of the juvenile distribution. In this approach, the interannual fluctuations in these distributions could not be taken into account and it was necessary to work on the whole database without using the 'year' component. The consequences of this decision will be discussed.

A statistical approach based on analyses of variance (ANOVA) and GLM has been used to describe these juvenile distributions according to factors known to govern their presence (nursery sector, bathymetry and sediment structure, see below).

As explained before, the high proportion of zero values leads to work on strata for which at least 10 trawl hauls are pooled. The problem is that as a result of response data pooling for ANOVA and GLM, data are not numerous enough to work directly on bathymetry (in meters) because there are not enough (≥ 10) trawls per meter of depth. Even the eight classes of bathymetry, used to study the seasonal variations of flatfish juvenile distributions in the first part of the work do not lead to 10 or more hauls per stratum. It is for this reason that it was decided to use the following bathymetric classes to pool the data for the ANOVA and GLM (in meters): < 5 , $[5, 10[$, $[10, 20[$, ≥ 20 . Hence, a stratum is defined by a sector, a class of bathymetry and the sediment structure.

Within these strata, if trawl hauls are pooled, there would be only one value of juvenile density per stratum. The variability between the trawl hauls is lost and it would not be possible to study the crossed effects between factors in ANOVA and GLM approaches. To maintain the intra-stratum variability expressed in the beam trawl haul data, the following method is used: For each stratum, 10 hauls are bootstrapped (ten fold, a haul is randomly selected with replacement). The average density calculated from these ten hauls is then used as one point data in the bootstrapped data set. For each stratum, this method (bootstrap then average) is repeated 100 fold. There are therefore 100 data for each stratum in this new data set and the analyses are undertaken using balanced tables.

The analyses of variance have been undertaken on this bootstrapped data set with the log-transformed pooled densities as the response variable. For the GLM approach, the same bootstrapped data set is used, and a preliminary approach allows to choose the law of distribution of the response variable.

Last, the results of the models of juvenile distribution were included in a GIS to calculate a relative index of the average juvenile abundance based on the extent of the strata geographic surfaces. A GIS is used with the following data:

- a map of the sediment structure of the Eastern Channel (Larsonneur et al., 1982) simplified into three classes of sediment,
- a map of the bathymetry (*Service hydrographique et océanographique de la Marine*, France) with the coastline and three isobaths: 5, 10, and 20 m,
- the limits between the nursery sectors.

Combining these three levels of information allows the strata to be identified and the area of each stratum to be calculated. As the GLM model allows to obtain a value of average density per stratum, the product of this average density and the corresponding area suggests a number of juveniles.

It is therefore possible to calculate the respective contributions of the different sectors using the following method:

- the surface of each stratum (sector \times bathymetric class \times sediment structure) is calculated using the GIS,
- for each stratum, the average number of juveniles is calculated from the product of this surface area and the corresponding modelled average density,
- these products per stratum are summed per sector and these values are used as nominal capacities of each sector.

3. RESULTS

3.1. Spatio-temporal fluctuations of juvenile abundance for sole and plaice

3.1.1. Seasonal distributions

Two main conclusions proceed from the cumulated frequency of juvenile densities according to depth (cf. 2.3) per season in the Eastern Channel (*figure 2*):

- All year long, flatfish nursery grounds are coastal, located in shallow waters. Beyond a depth of 20 m, there are almost no juvenile flatfish (less than 1% of the cumulated frequency), with the higher densities being found in less than 8 m depth for sole and less than 12 m depth for plaice.
- There are few seasonal variations of this distribution. In spring and in autumn these distributions are similar for positive bathymetric classes but 1-group individuals are more numerous close to the shore. Comparison of autumnal and spring cumulative frequencies with a Wilcoxon rank test does not allow the separation of these distributions. In winter, when fewer data are available for the single Seine Estuary, conflicting results are obtained for sole and plaice. Sole seems to be closer to the shore in autumn than in winter but it is the opposite for plaice. The Wilcoxon rank test does not show significant differences between these autumn and winter distributions.

Unlike in other areas where winter distributions are notably deeper than those in autumn (review in Gibson, 1997), juvenile flatfish distribution is coastal all year long in the Eastern Channel. Thus, the following analysis of juvenile distribution is based solely on autumn data. This season represents the distribution of juvenile flatfish during the period of growth, and is most appropriate for the study of nursery grounds (Dorel et al., 1997), and is also the most documented (90% of the trawl hauls, *table I*) in our database. All of the following results are based solely on autumn surveys and will finally be discussed in relation to the situation for the other seasons.

3.1.2. Interannual fluctuations in juvenile distribution

Figure 3 shows the distribution of 1-group plaice from 1995 and 1997, years chosen as examples, calculated with a simple kriging method from all of the

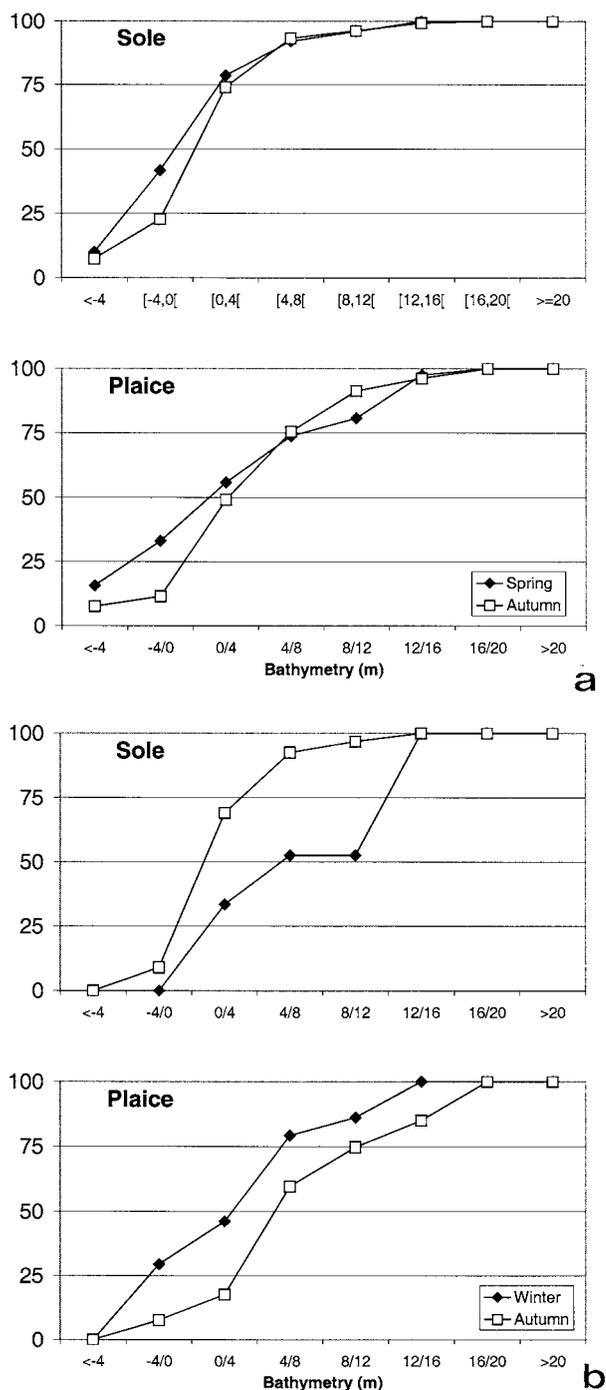


Figure 2. Sole and plaice juvenile distribution according to bathymetry (cumulated frequencies in%): in spring and in autumn on the French coasts of the Eastern Channel (a); in winter and in autumn in the Seine estuary (b).

available trawl hauls. For these years the English Coast, the Bay of Somme and the Bay of Seine are the areas sampled (table 1). Figure 3 confirms that plaice nursery grounds are located predominantly in shallow

waters. Moreover, figure 3 demonstrates the asynchronous interannual abundance variations of 1-group plaice between the different parts of the Eastern Channel in these two years, the location of high densities of juvenile plaice varying according to years: the number of juveniles appears greater in Rye Bay in 1995, but in 1997 they appear greater in the Bay of Seine and in the Bay of Somme. A similar pattern was observed for plaice for the other years when surveys are available (table 1), and also for the sole. Juvenile flatfish densities vary from year to year but also from one coastal sector to another, suggesting that, for a given year, the level of recruitment differs substantially over rather small distances.

In order to analyse these asynchronous variations, a MFA (cf. 2.3) has been undertaken. Figure 4a shows the two axis of the analysis undertaken on these data (100% of the total inertia for two variables), with trawling stations pooled according to their geographical origin. This analysis discriminates well between the different points (a sector \times a year) into three groups corresponding to the 3 sectors. This analysis confirms the results shown in figure 3, that among different sectors for the same stock, interannual fluctuations of juvenile densities are different.

Hence, the Eastern Channel has been separated into 10 sectors (figure 1), based on the physical parameters known to influence spatial fluctuations of recruitment, coastal morphology (Rijnsdorp et al., 1992), bathymetry (Gibson, 1997), sediment structure (Millner and Whiting, 1990; Howell et al., 1999; Gibson and Robb, 2000) and estuarine influence (Marshall and Elliot, 1998). These 10 sectors can be considered as homogeneous according to these criteria and, hence, as demonstrated on three of these sectors with the MFA, as coastal areas inside which there is a spatial coherence between year class strength.

3.1.3. Consolidation of sectors

The purpose of this analysis was to identify if adjacent sectors could be pooled into one based on the interannual fluctuations in juvenile densities. To study these variations, an MCA was undertaken with strata (a year \times one of ten predefined nursery sectors) as individuals, and the semi-quantitative pooled densities (cf. 2.3.) as variables. Figure 4b shows the two axes of this MCA (100% of inertia) with the positions of the sectors (averaged over years). The sectors 'Dieppe-Antifer' and 'Calvados' are not included in this analysis because there were fewer than 10 trawl hauls completed in these sectors for a given year. Three adjacent sectors (Boulogne, Bay of Somme, Tréport-Dieppe) appear together using this approach, suggesting that interannual variations in sole and plaice pre-recruit abundance are synchronous between these areas. These sectors were therefore combined into one, which we called the 'South East' sector (figure 1). No other adjacent sectors had synchronous interannual fluctuations in juvenile abundance. Therefore, the Eastern Channel was divided into 8 sectors within

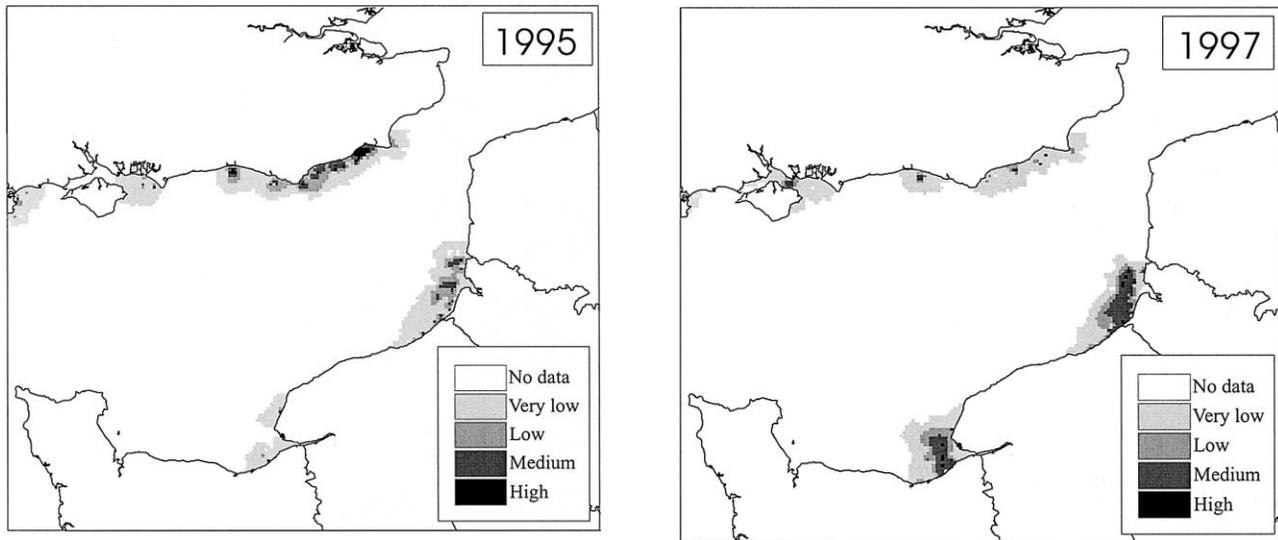


Figure 3. Interpolated map of log-transformed plaice densities, $y = \ln(x + 1)$, for the years 1995 and 1997.

which interannual fluctuations of juvenile abundance in nursery grounds appeared to be synchronous.

3.2. Average densities on the costal areas

3.2.1. Choice of the model

The purpose of this research was to study the sole and plaice juvenile abundance according the environmental factors known to govern their presence on nursery grounds (bathymetry, estuarine influence and sediment structure, cf. 3.1.2.) in order to obtain a quantitative description of the different coastal areas as nursery grounds. The 8 sectors identified (cf. 3.1.3.) are considered as homogeneous with regard to fluctuations in interannual juvenile flatfish densities. Moreover, a combination of factors such as their location relative to spawning areas and currents or anthropogenic disturbance means that these different areas do not have the same potential as nursery grounds. So, they have to be included as descriptors in the model. These sectors can also be considered as a descriptor of the estuarine influence as the river flow is very different from a sector to another (table II). Therefore, to analyse the juvenile flatfish distribution with regard to the bathymetry, the sediment structure, the estuarine influence and the respective potential of the different coastal sectors, it is possible to use only three descriptors: homogeneous coastal sector, bathymetry (in classes, cf. 2.3.) and sediment structure. The following ANOVA and GLM approaches are completed using a bootstrapped dataset where a stratum (≥ 10 hauls) consists of a combination between a sector, a class of bathymetry and a class of sediment structure (cf. 2.3.) Figure 2 shows that sectors where depth is greater than 20 m cannot be considered as nursery grounds. For this reason they are not included in this statistical approach.

An analysis of variance has been undertaken for each species on the bootstrapped data set with the log-transformed pooled densities as the response variable and the homogeneous sectors, the bathymetric classes and the sediment classes as the descriptors (cf. 2.3.). The same result is obtained for both species with the three main effects of the studied factors being significant as well as the interaction of sector and bathymetry. This interaction is logical because the juvenile depth distribution is different from one sector to another (Symonds and Rogers, 1995).

To analyse the distribution of the response variable (cf. 2.3.), the average (μ) and the variance (σ^2) are calculated for each stratum (a sector \times a bathymetric class \times a sediment class) on the 100 pooled densities obtained with the bootstrap method (cf. 2.3.). The relation between $\ln(\mu)$ and $\ln(\sigma^2)$ is examined for the data set (a point (μ, σ) per stratum) using linear regression. The relation obtained ($r^2 = 96\%$ for the sole and 97% for the plaice), $\sigma^2 = \alpha \times \mu^\beta$ with β close to 2 (2.1 for both sole and plaice) suggests a gamma distribution. A χ^2 test of the goodness of fit (S-Plus software `chisq.gof` standard function) cannot exclude the possibility that the distribution of our response data (pooled densities) belongs to the gamma family.

3.2.2. Relations between environmental factors and juvenile settlement

According to the ANOVA and to the study of the law of the response variable, the model used to quantify juvenile distribution is the following generalized linear model used with a gamma distribution of the response variable:

$$\frac{1}{\text{Density}_{\text{Sect,Sed,Bat}}} = \alpha_1 \times \text{Sect} + \alpha_2 \times \text{Sed} + \alpha_3 \times \text{Bat} + \alpha_4 \times (\text{Sect} \times \text{Bat}) + \alpha_5$$

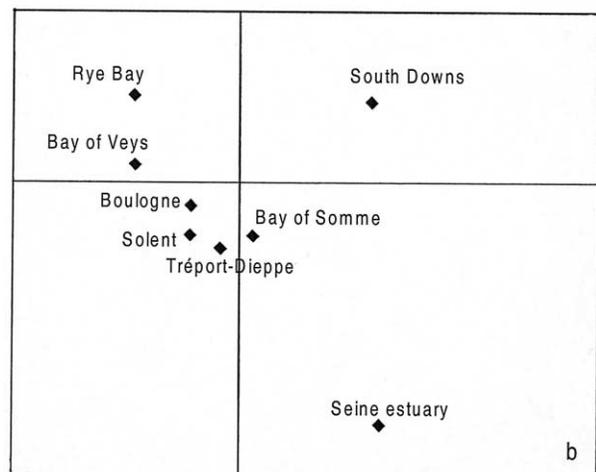
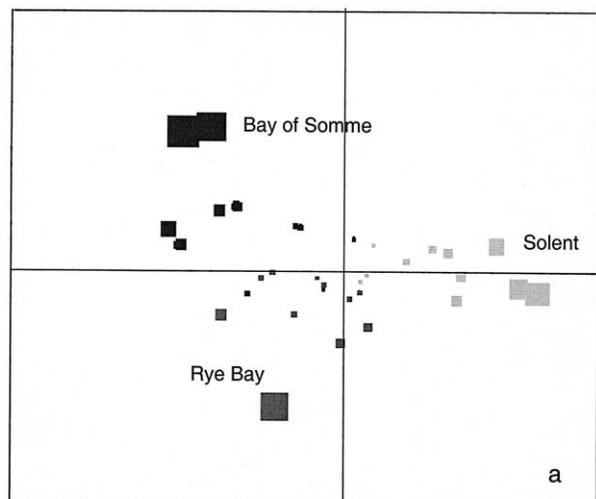


Figure 4. Factorial plans of multivariate analyses. **a.** Multifactor analysis of three different coastal sectors. Each square represents data for a single year and a single sector (average position on the corresponding trawling station). The size of the square represents its relative contribution and its shading represents its sector. **b.** Data for all years combined within sectors on a multi-correspondence analysis. Average position on the different years per sector

with the response variable:

– $Density_{Sect,Sed,Bat}$: bootstrapped pooled density of the 1-group juveniles (sole or plaice),

and the descriptors:

– $Sect$: sector effect,

– Sed : sediment structure effect,

– Bat : bathymetry effect,

– $Sect \times Bat$: sector \times bathymetry crossed effect,

– α_i : parameters of the model.

The response variable is the inverse of the studied density because the inverse link is the natural one for gamma distributions in GLM. The explained deviance is 34% for the sole and 26% for the plaice and the residuals fit with a gamma family distribution.

3.3. Mapping juvenile distributions

The results of the model were included in a GIS to calculate a relative index of the average juvenile abundance based on the extent of the strata geographic surfaces (cf. 2.3.). If the structure of the model allows a potential average density per stratum (sector \times bathymetric class \times sediment structure) to be estimated (figure 5), for a few strata the model does not allow this calculation because:

– there are not enough trawl hauls per stratum (≤ 10) for the sector Dieppe–Antifer, the descriptor ‘sector’ cannot be tuned and the models cannot supply predicted values,

– for a given sector, if a bathymetric class is not available (less than ten trawl hauls), the effect of the crossed factor, sector \times bathymetric class, cannot be calculated and it is not possible to obtain predicted values, for this reason there are no values for the two lower bathymetric classes in the sector called Calvados and in the middle bathymetric class for the sector Bay of Veys.

Nevertheless, the average density of juveniles in the Eastern Channel is estimated for more than 90% of the area of the potential nursery grounds (depth < 20 m).

Using this method, the depth/sediment strata that support the highest sole and plaice densities have been identified (figure 5). In general, high densities of both 1-group sole and plaice occur in the inshore waters of the Bay of Somme, to 20 m depth off the South Downs. In addition, 1-group sole are found in high

Table II. Average numbers of sole and plaice juveniles within coastal sectors in ICES division 7D.

Sector	Annual average river flow ($m^3 \cdot s^{-1}$)	Sole (%)	Plaice (%)
Bay of Veys	60	10	5
Calvados	40	0	0
Seine Estuary	500	4	7
South East	50	36	48
Rye Bay	5	15	12
South Downs	5	16	13
Solent	5	18	15

Numbers of sole and plaice juveniles are reported as percentages of total 1-group juveniles.

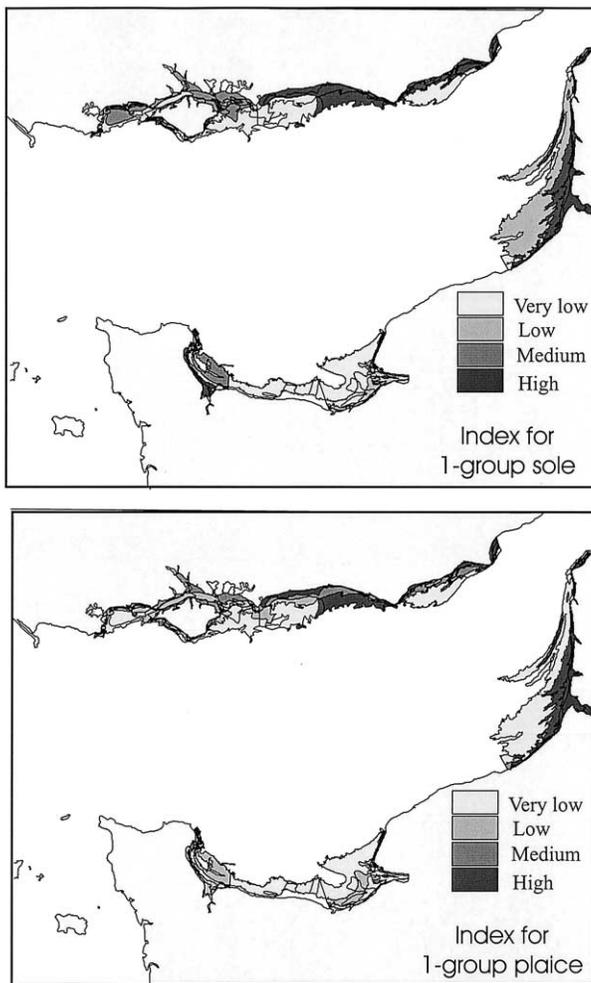


Figure 5. Index of potential density for 1-group sole and plaice.

densities in inshore waters of the Bay of Veys and Rye Bay. The respective contributions of the different sectors (*table II*) show the main role played by the sector called South East (*figure 1*) in supplying Eastern Channel flatfish stocks (36% of the average quantity of juvenile for the sole and 48% for the plaice). These data also show that nursery grounds are not necessarily associated with estuarine areas. The comparison between the average river flow per sector (*table II*) and the main nursery sectors calculated in *figure 5* and *table II* confirms the distributions of row densities presented for 1995 and 1997 on *figure 3*: English sole and plaice nursery grounds with the highest densities (Rye Bay and parts of the South Downs Coast) have very little freshwater influence. For these two species, the main estuarine sector, the Seine Estuary, has a relatively low contribution to the total juvenile quantity as the juvenile distribution is not concentrated in the small areas influenced by rivers.

4. DISCUSSION–CONCLUSION

4.1. Different nursery sectors for a same stock

The study of spatio-temporal juvenile densities in the Eastern English Channel shows that between neighbouring coastal areas, there are no consistent patterns of recruitment variability. It is nevertheless possible to separate the Eastern English Channel into a number of coastal sectors inside which there is a spatial coherence in year class strength. Rijnsdorp et al. (1992) have already demonstrated that the factors determining recruitment vary over a relatively small spatial scale of less than 100 or 200 km. Interannual variability in the hydrodynamic circulation between spawning and nursery grounds appears to be a key factor in this spatial heterogeneity of recruitment strength (Nielsen et al., 1998). It explains that, as observed in this study for the south-eastern sector, the similarity in recruitment pattern is restricted to those nursery areas which have a similar direction of the coastline (Rijnsdorp et al., 1992).

Hence, it seems logical to divide the coastal zone into several sectors considered as homogeneous with regards to recruitment variability. The value of this division has been demonstrated, taking into account these separate sectors to improve the recruitment prediction from coastal surveys for the sole in the Eastern Channel (Riou et al., 2000).

Therefore, it is also logical to take this division into account in a model approach of flatfish distribution. Moreover, it allows the study of estuarine influence on juvenile flatfish distribution.

4.2. From a simple model using autumnal surveys to a general typology

This modelling approach allows us to describe coastal nursery grounds in relation to their physical properties. There are of course other descriptors, such as food availability, that are known to influence juvenile distributions. Nevertheless the descriptors used here are the only ones available for the whole area, allowing a model-GIS coupled approach. Therefore, if these results cannot be analysed as an exhaustive causal study of flatfish juvenile distribution, they are nonetheless useful to describe these distributions according to well known parameters.

Unlike in other areas where winter distributions are notably deeper than those in autumn, juvenile flatfish distributions in the Eastern Channel are coastal all year long. This stability in the juvenile distribution seems to be specific to the Eastern Channel and can be explained by the hydrodynamic properties of this area. In other systems, the juveniles move to deeper areas in winter to find warmer water (review in Gibson, 1997). In the Eastern Channel, due to strong tidal currents and moderate depths (< 40 m almost everywhere) there are no thermal gradients from the coast to deeper waters in autumn and winter (Hoch and Garreau, 1998).

It is therefore possible to analyse juvenile distributions using only autumnal survey data and to consider these results valid throughout the year. Without seasonal migration, exchange between nursery sectors is unlikely and the results for 1-group flatfish will be similar to those of 0-group. Even if the 0-group distribution is more coastal than the 1-group distribution (Riley et al., 1981, Rogers and Millner 1996, Morin et al., 1997), the comparison between the different sectors is valid for the youngest fish.

4.3. Contributions of the different coastal sectors

For plaice, exchange of individuals between ICES Division 7D and the adjacent areas is important, although part of the stock seems to be resident (Anonymous, 1999). For sole, the rates of exchange seem to be less than for plaice (Anonymous, 1993) and Eastern Channel nurseries are generally considered to supply recruits for the Eastern Channel sole stocks. The fact that the level of recruitment is related to the respective surface of the nursery grounds (Rijnsdorp et al., 1992; Gibson, 1994) and to the juvenile densities, depending on habitat quality (Gibson, 1994), has already been demonstrated (reviewed in Van der Veer et al., 2000). Hence, at least for the sole, if this cartography allows to estimate the relative number of flatfish juvenile in different coastal sectors, it can be used to assess the relative influence of these different coastal nursery sectors for flatfish stocks in the Eastern Channel.

Nevertheless, in this description, the asynchronous fluctuations of abundance between the different nursery sectors are not taken into account, so that the models are only based on average multi-annual distributions. It is the reason why the intra-stratum variability is important and allows to understand why the models only explain a low proportion of the juvenile distribution (34% for the sole and 26% for the plaice). However, from year to year, the contribution of each nursery can vary considerably. Thus, for a given year, it is not possible to predict precisely which nursery ground will make the greatest contribution.

4.4. Eastern Channel specificity

In the Eastern Channel, juvenile distribution appears to be specific to certain areas, relative to other studied areas. First, as explained in 4.2., due to the lack of thermal gradients from the coast to deeper waters, there are few detectable seasonal variations of flatfish juvenile distribution. Moreover, juvenile flatfish are not concentrated in estuarine areas. This last result can be related to the physical structure of this system. Shallow and unstratified, this system is very productive with regard to continental shelf waters (Hoch and Garreau, 1998) and the most estuarine sectors are not the most productive. Comparison of diatom biomass maps during the productive period (Hoch and Garreau, 1998) and juvenile flatfish average quantity (*figure 5*) shows that, as concluded by Friedland et al. (1996) and

Thiel et al. (1997) on other species and other nursery sectors, the productivity level fits with juvenile flatfish distribution in the Eastern Channel. Nursery grounds are the more productive sectors but not the most estuarine ones.

4.5. Interest of this modelling approach

Compared with an interpolation of the available data, such a modelling approach has several advantages:

- This method of quantitative description of the flatfish distribution based on environmental factors allows a spatial stratification of the coastal zone into different nursery grounds.
- It also allows interpolation of data into areas where the descriptive environmental factors are known but where sampling data are too sparse. For a few strata, the model cannot estimate a potential density because the number of hauls is insufficient (cf. 3.3). Nevertheless, this method allows some assessment of areas sparsely covered by surveys and, hence, to give a general diagnosis based on more than 90% of the coastal area.
- Such a method of interpolation, based on descriptors known throughout the study area, provides a relative index of the average juvenile abundance based on the extent of the respective geographic surfaces and, hence, an assessment of the contribution of different sectors to the common stock.

This work demonstrates the important role played by the English and French eastern sector for the Eastern Channel. These results can be used for coastal zone management, for a quantified hierarchy among different coastal areas is an important tool for manager decisions.

Habitat quality varies depending upon anthropogenic factors and quality assessment may help prevent loss of those areas essential to sustain fish populations (Meng et al., 2000). For this reason it is important to identify the habitat type important to flatfish species. The recent studies of the environmental effects of trawling and their consequences for the benthic fauna and the trophic chain show that some access restriction for trawlers and dredgers can improve the carrying capacity of potential nurseries (Kaiser and de Groot, 1999, Hall, 1999). Moreover, closing some areas to fishing activities can increase their respective contribution to stock recruitment (Paastors et al., 1998). Hence, the comparison of these results with maps delimiting the regulation of access to the coastal zone can identify the degree of overlap between potentially conflicting activities (fishing but also other potentially harmful activities as dredging, construction, etc.) and key sites of importance to the early life-history stages of commercial flatfish (Le Pape et al., 2000).

This method can also be used to study other species and other areas. A comparable method, using regression quantile estimates to re-code the environmental raster maps to produce maps of habitat suitability, has also been used for spawning habitats suitability for the

sole in the eastern part of the Eastern Channel (Eastwood and Meaden, 2000). The method applied here, using the re-sampling bootstrap, is a valuable means of analysing data coming from different surveys collected with different sampling effort. Physical parameters to include in the model will depend on the ecology of the stocks and on the properties of the study site, as the degree of precision in surface computing is related to the size of the studied area and to the precision of the available maps.

Acknowledgements. This project was carried out with the financial assistance of the European Commission (contract EU DG XIV-97/030, it does not necessarily reflect the views of the commission and in no way anticipates the opinion of the commission in this area; not to be reproduced unless the source of the material, Le Pape et al., 2000, is indicated), the French region Basse Normandie and the French Water Agency – Seine Normandie, Ifremer, and the Ministry of Agriculture, Fisheries and Food, UK. We would like to thank Jacques Populus (Ifremer) for his contribution to the GIS, Yves Desaunay (Ifremer) and Rachid Amara (*Université du Littoral*, France) for their consideration of ecological processes, Philippe Gros (Ifremer) and Stéphanie Mahévas (Ifremer) for their helpful methodological advice, and the anonymous reviewers for their fruitful suggestions.

References

- Anonymous, 1993. Biogeographical identification of English Channel fish and shellfish stocks. Ifremer Report DRV-93028. Éditions Ifremer, Plouzané.
- Anonymous, 1999. Report of the working group on the assessment of demersal stocks in the North Sea and Skagerrak, ICES CM1999/ACFM:8. ICES, Copenhagen.
- Beillois, P., Desaunay, Y., Dorel, D., Lemoine, M., 1979. Nurseries littorales de la baie du Mont-Saint-Michel et du Cotentin Est. Rapport de l'Institut des sciences et techniques des pêches maritimes. Ifremer, Nantes.
- Costanza, R., Darge, R., Degroot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., Oneill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., Vandenbelt, M., 1997. The value of the world's ecosystem services and natural capital. *Nature* 387, 253–260.
- Creutzberg, F., Duineveld, G.C.A., Van Noort, G.J., 1987. The effect of different numbers of tickler chains on beam-trawl catches. *J. Cons. ICES* 43, 159–168.
- Dorel, D., Beillois, P., Desaunay, Y., Guérault, D., 1985. Évaluation expérimentale des composantes de la capturabilité d'un chalut à perche échantillonneur utilisé pour l'estimation d'abondance des juvéniles de soles. ICES CM/G: 40. ICES, Copenhagen.
- Dorel, D., Koutsikopoulos, C., Desaunay, Y., Marchand, J., 1997. Seasonal distribution of young sole (*Solea solea* (L.)) in the nursery ground of the Bay of Vilaine (Northern Bay of Biscay). *Neth. J. Sea Res.* 27, 297–306.
- Eastwood, P.D., Meaden, G.J., 2000. Spatial modelling of spawning habitat suitability for the sole (*Solea solea* L.) in the eastern English Channel and southern North sea. ICES CM/N05. ICES, Copenhagen.
- Escofier, B., Pagès, J., 1994. Multiple factor analysis (AF-MULT package). *Comput. Stat. Data Anal.* 18, 121–140.
- Fanning, L.P., 1994. Intercalibration of research survey results obtained by different vessels. Canadian Atlantic Fisheries Scientific Advisory Commission (CAFASC), Dartmouth.
- Friedland, K.D., Ahrenholz, D.W., Guthrie, J.F., 1996. Formation and seasonal evolution of Atlantic menhaden juvenile nurseries in coastal estuaries. *Estuaries* 1, 105–114.
- Gibson, R.N., 1994. Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. *Neth. J. Sea Res.* 32, 191–206.
- Gibson, R.N., 1997. Behaviour and the distribution of flatfishes. *Neth. J. Sea Res.* 37, 241–256.
- Gibson, R.N., Robb, L., 2000. Sediment selection in juvenile plaice and its behavioural basis. *J. Fish Biol.* 56, 1258–1275.
- Halgand, D., Arzul, G., Cochard, M.L., Erard-Le-Denn, E., Huet, J., Le Claire, J., Quiniou, F., 1998. Surveillance écologique et halieutique de l'environnement marin du site de la centrale de Penly (Manche Est). Ifremer Rep. DRV 99-06. Ifremer, Plouzané.
- Hall, S.J., 1999. The effects of fishing on marine ecosystems and communities. Fish biology and aquatic resources series 1. Blackwell Scientific Publications Ltd, Oxford.
- Hanson, J.M., 1996. Seasonal distribution of juvenile Atlantic cod in the southern gulf of St Lawrence. *J. Fish Biol.* 49, 1138–1152.
- Hoch, T., Garreau, P., 1998. Phytoplankton dynamics in the English Channel: a simplified three-dimensional approach. *J. Mar. Syst.* 16, 133–150.
- Howell, P.T., Molnar, D.R., Harris, R.B., 1999. Juvenile winter flounder distribution by habitat type. *Estuaries* 22, 1090–1095.
- Kaiser, M.J., de Groot, S.J., 1999. The effects of trawling on non-target species and habitats: biological, conservation and socio-economic issues. Blackwell Scientific Publications Ltd, Oxford.
- Kuipers, B., 1975. On the efficiency of a two meter beam trawl for juvenile plaice (*Pleuronectes platessa*). *Neth. J. Sea Res.* 9, 69–85.
- Larsonneur, C., Bouysse, P., Auffret, J.P., 1982. The superficial sediments of the English Channel and its western approaches. *Sedimentology* 29, 1–14.
- Le Pape, O., Riou, P., Rogers, S., Carpentier, A., Coppin, F., Morin, J., Lemoine, M., 2000. Nursery grounds in the coastal zone of the Eastern English Channel: typology and management measures. Ifremer report, EU Contract DG XIV 97/0030. Ifremer, Plouzané.
- Marshall, S., Elliot, M., 1998. Environmental influences on the fish assemblage of the Humber estuary, U.K. *Estuar. Coast. Shelf Sci.* 46, 175–184.

- Meng, L., Gray, C., Taplin, B., Kupcha, A., 2000. Using winter flounder growth rates to assess habitat quality in Rhode Island's coastal lagoons. *Mar. Ecol. Prog. Ser.* 201, 287–299.
- Mesnil, B., 1983. Indices d'abondance des juvéniles de poissons plats devant les côtes françaises de Manche Est et de mer du Nord. ICES CM/G:55. ICES, Copenhagen.
- Millner, R.S., Whiting, C.L., 1990. Distribution and abundance of juvenile sole and plaice in the eastern English Channel from young fish surveys. ICES CM/G:38. ICES, Copenhagen.
- Morin, J., Riou, P., Lemoine, M., Le Pape, O., Bessineton, C., Vedieu, C., Simon, S., 1997. Étude des nourriceries de la baie de Seine orientale et de l'estuaire de la Seine. Synthèse des connaissances. Convention d'aide à la recherche n° 96/1212618BMF avec la Préfecture de région de Haute-Normandie et le Port autonome du Havre.
- Nielsen, E., Bagge, O., MacKenzie, B.R., 1998. Wind-induced transport of plaice (*Pleuronectes platessa*): early life history stages in the Skagerrak-Kattegat. *J. Sea Res.* 39, 11–28.
- Paastors, M.A., Rijnsdorp, A.D., van Beck, F.A., 1998. Evaluation of the effects of closed areas on fish stocks. ICES CM/U2. ICES, Copenhagen.
- Parrish, F.A., De Martini, E.E., Ellis, D., 1997. Nursery habitat in relation to production of juvenile snapper, *Pristipomoides filamentosus* in the Hawaiian Archipelago. *Fish. Bull.* 95, 137–149.
- Porch, C.E., Scott, G.P., 1994. A numerical evaluation of GLM methods for estimating indices of abundance from West Atlantic bluefin tuna catch per trip data when a high proportion of the trips are unsuccessful. ICCAT coll. Vol. scient. Pap. 42, 1–6.
- Porch, C.E., 1995. Porch, C.E., numerical evaluation of GLM methods for estimating indices of abundance from West Atlantic small bluefin tuna catch per trip data when the data are aggregated to minimize zero catches. ICCAT coll. Vol. Scient. Pap. 44, 1–5.
- Rijnsdorp, A.D., Van Beek, F.A., Flatman, S., Millner, R.M., Riley, J.D., Giret, M., De Clerck, R., 1992. Recruitment of sole stocks, *Solea solea* (L.), in the Northeast Atlantic. *Neth. J. Sea Res.* 29, 173–192.
- Riley, J.D., Symonds, D.J., Woolner, L., 1981. On the factors influencing the distribution of 0-group demersal fish in coastal waters. ICES Repory no. 178. ICES, Copenhagen, pp. 223–238.
- Riou, P., 1999. Dynamique des nourriceries de sole et de plie en Manche Est. Importance écologique de l'estuaire de la Seine. Thèse de doctorat. Université de Caen, Caen.
- Riou, P., Le Pape, O., Rogers, S., Lemoine, M., 2000. Intérêt de l'étude des nourriceries de soles (*Solea solea*) et de plies (*Pleuronectes platessa*) à l'échelle de la Manche Est (Division CIEM 7D). Application à l'identité de stock et à l'estimation du recrutement. Les espaces de l'halieutique, 4^e forum halieumétrique de l'Association française d'halieumétrie. IRD Éditions, Bondy, pp. 99–123.
- Rogers, S.I., Millner, R.S., 1996. Factors affecting the annual abundance and regional distribution of English inshore demersal fish populations:1973 to 1995. *ICES J. Mar. Sci.* 53, 1094–1112.
- Symonds, D.J., Rogers, S., 1995. The influence of spawning and nursery grounds on the distribution of sole *Solea solea* (L.) in the Irish Sea, Bristol Channel adjacent areas. *J. Exp. Mar. Biol. Ecol.* 190, 1–19.
- Thiel, R., Nellen, W., Sepulveda, A., Oesmann, S., Tebbe, K., Drenkelfort, T., 1997. Spatial gradients of food consumption and production of dominant fish species in the Elbe estuary, Germany. ICES CM/S:04. ICES, Copenhagen.
- Van der Veer, H.W., Berghahn, R., Miller, J.M., Rijnsdorp, A.D., 2000. Recruitment in flatfish, with special emphasis on North Atlantic species: progress made by the flatfish symposia. *ICES J. Mar. Sci.* 57, 202–215.