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Quantitative description of habitat suitability for the juveniles of seven estuarine and coastal dependent fish species in the Bay of Biscay

Par : Émile TRIMOREAU

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Synthesis

Estuaires et zones côtières sont importants pour de nombreuses espèces de poissons de par leur fonction de nourriceries et donc d'habitats essentiels. Ces zones riches en juvéniles permettent en effet le renouvellement du stock par la production d'individus adultes. La diminution et la dégradation de l'habitat sont des phénomènes répandus dans ces zones qui concentrent une forte activité humaine. Elles doivent donc être protégées pour le renouvellement des populations. Des modèles d'habitats ont donc été développés afin de prédire les densités observées de juvéniles de 7 espèces (*Solea solea*, *Pleuronectes platessa*, *Dicologlossa cuneata*, *Chelidonichthys lucernus*, *Mullus surmuletus*, *Merlangius merlangus* et *Trisopterus luscus*) dépendantes des zones côtières et estuariennes dans 6 nourriceries du golfe de Gascogne (Estuaires de la Vilaine, de la Loire et de la Gironde, baie de Bourgneuf, Pertuis d'Antioche et Pertuis Breton). Bathymétrie, sédiment, salinité de surface et hauteur de vagues ont été utilisés comme variables explicatives. Une cartographie des densités prédites a ensuite été réalisée afin d'identifier les habitats essentiels concentrant de fortes densités de juvéniles.

Cette étude regroupe 25 années de campagnes scientifiques de chalutage de fond conduites dans le Golfe de Gascogne de 1980 à 2011. Les traits de chaluts on été standardisés par sélection selon des critères de période (Automne : fin août à mi-octobre), engin (Chalut à perche de 3m d'envergure, mailles étirées de 20mm à l'extrémité), durée (Entre 10 et 15 minutes), validité (Pas de fort colmatage ni de déchirure). Au total, 1643 traits de chaluts réalisés sur 6 nourriceries et provenant de 3 sources différentes ont été retenus. Les données de captures ont été restreintes aux juvéniles de moins de 1 an grâce à l'emploi d'une taille maximale pour chaque espèce, obtenues par bibliographie et observation des histogrammes de captures. Le nombre de juvéniles capturés ainsi obtenu a été corrigé par un facteur de sélectivité dépendant de la taille des poissons capturés. Les captures corrigées ont ensuite été converties en densité en les divisant par la surface des traits de chaluts.

Des données concernant les paramètres physiques sélectionnés ont été rassemblées de manière exhaustive sur toute la zone d'étude afin de constituer des variables explicatives cohérentes. La bathymétrie, disponible sur une grille de 463m de côté, a été découpée en 4 classes (] -36m ; -20m],] -20m ; -10m],] -10m ; -5m] et > -5m). Le type de sédiment a été réparti en 3 classes selon la taille des grains (Vase, sable fin et sable grossier). La salinité de surface, disponible en psu (Practical Salinity Unit) sur une grille de 4km de côté de 1980 à 2011, a été moyennée pour chaque année sur la période de janvier à avril (période d'enrichissement des zones estuariennes par apport fluviaux étroitement liés à la répartition des juvéniles) et découpée en 3 classes (Zone estuarienne : < 30 psu, zone mixte : entre 30 et 32 psu et zone marine : > 32 psu). La hauteur de vague, disponible de 2002 à 2011 seulement, sur une grille de 2km de côté, a été moyennée sur toutes les années et sur la période de mai à août (période estivale de croissance des juvéniles sur les nourriceries).

Les paramètres physiques et les densités calculées ont été insérés dans des tables géoréférencées grâce à une base de données postgreSQL. Les positions des traits de chaluts ont été croisées avec les paramètres physiques afin d'associer les valeurs de ces derniers à chaque densité calculée.

Les modèles d'habitat ont été construits grâce à la méthode delta. Une distribution binomiale a été ajusté sur la probabilité de présence et une distribution gaussienne a été ajustée sur les densités positives log-transformées. La densité estimée a été obtenue par le produit des estimateurs de la probabilité de présence et du logarithme de la densité, ainsi que de la correction de Laurent. Les effets simples et croisés de tous les paramètres physiques, ainsi que du secteur et de l'année de réalisation des traits de chaluts ont été testés. Le choix de la significativité a été basée sur le seuil de 5% pour l'erreur de type 1 et sur les AIC des modèles. La méthode delta ne permettant pas une interprétation directe des effets des facteurs, ceux-ci ont été recalculés. Un processus de validation a été suivi en séparant le jeu de données en un jeu de calibration (75%), sur lequel les modèles ont été ajustés, et un jeu de validation (25%), sur lequel des densités ont été estimées grâce aux modèles précédemment ajustés. L'ajustement des observations par rapport aux prédictions a été comparé entre les deux jeux de données.

Une table géoréférencée regroupant les différents paramètres physiques, ainsi que les limites des secteurs, et couvrant toute la zone d'étude a été créée. Les densités de juvéniles ont ainsi pu être prédites sur toute la zone d'étude grâce aux modèles ajustés précédemment. Trois scénarii de panache estuarien ont été testés et les contributions des différents types d'habitat aux populations totales de juvéniles ont été calculées. Les densités ont été visualisées sous forme de cartes grâce au logiciel postGIS.

Seuls les poissons plats on été retenus pour la cartographie, les autres espèces ayant été rejetées pour cause de rareté ou de non correspondance entre la zone d'étude et l'aire de répartition. Le processus de validation a appuyé la robustesse de la méthode pour toutes les espèces.

Seuls les facteurs simples ont été retenus à part la hauteur de vague dans le cas de *Pleuronectes platessa* (probabilité de présence) et *Dicologlossa cuneata* (probabilité de présence et densités positives). Le secteur n'a pas non plus été retenu dans le cas de *Dicologlossa cuneata* (densités positives).

L'observation des effets moyens a révélé le caractère structurant de la bathymétrie, du sédiment et de la hauteur de vague pour *Solea* solea et *Pleuronectes platessa*. Les densités sont maximales pour la classe de faible bathymétrie, de sédiment vaseux et de faible hauteur de vague et chutent rapidement pour les classes supérieures. *Dicologlossa cuneata* présente des effets différents, avec un effet prépondérant du sable fin. Les effets secteur et année révèlent des tendances spatiales et temporelles fortes pour *Pleuronectes platessa* et *Dicologlossa cuneata*. La diminution du Nord vers le Sud pour *Pleuronectes platessa* et l'augmentation respective pour *Dicologlossa cuneata* sont liées aux limites de répartition de ces deux espèces. Les tendances temporelles ont été expliquées par un changement dans la température de surface des eaux sur la zone d'étude.

Les zones peu profondes et vaseuses abritent 60% de la population totale des juvéniles de *Solea solea* et *Pleuronectes platessa* alors qu'elles ne représentent que 16% de la zone étudiée. Elles peuvent donc être considérées comme des habitats essentiels pour ces deux espèces. Les zones profondes (] -36m ; -20m]) peuvent par ailleurs être considérées comme inadaptées pour la fonction de nourricerie.

Outre le processus de validation, la méthode utilisée peut être qualifiée de robuste de par les similarités observées entres les résultats de cette étude et les résultats précédents concernant *Solea solea*. En effet, malgré l'ajout de nouvelles données, les mêmes conclusions peuvent être tirées dans le cas de cette espèce.

La variabilité résiduelle non expliquée peu provenir de différentes sources, en particulier les apports larvaires. Ces apports peuvent être sources de variabilité spatiale, les différents secteurs ne recevant pas la même quantité de larves, et de variabilité temporelle, le nombre d'œufs pondu variant chaque année.

Cette étude a soulevé des problèmes de restriction de la zone échantillonnée lors des campagnes. Les zones rocheuses n'étant pas couvertes, pour des raisons de dégradation du matériel de pêche, les espèces vivant aussi sur les fonds rocheux ne peuvent pas être représentées convenablement. D'autre part, les campagnes scientifiques sur les nourriceries côtières et estuariennes ne sont pas étendues au large et les espèces avec des aires de répartition plus larges ne sont pas non plus étudiables.

Au final, les zones peu profondes, recouvertes de sédiments fins et abritées sont les habitats essentiels des poissons plats dans le golfe de Gascogne. Elles doivent être protégées en priorité dans le cadre du renouvellement des populations.

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Summary

1. Introduction: The need for a clear identification of fish nursery grounds.

Estuaries and coastal areas are important for many fish species due to their habitat function as nursery spots (Able, 2005). The carrying capacity and quality of these habitats influence juveniles' growth and survival rates (Rijnsdorp et al., 1992; Gibson, 1994; Iles and Beverton, 2000). Pollution and habitat destruction caused by human activity are known to affect ecosystems and thus strongly impact the recovery of fish stocks (Coleman et al., 2008; Diaz and Rosenberg, 2008; Halpern et al., 2008). Estuaries and coastal areas, by combining intense human activity and fish nursery grounds, are particularly affected by these phenomena (Rochette et al., 2010) and should therefore receive special consideration. The protection of such sites is required to maintain fish stocks at a reasonable level of biomass by protecting juveniles. It is therefore of importance to assess the relations between physical parameters, impacting on the capacity and quality of habitats, and fish density. Costal management, e.g. design of Marine Protected Areas (MPA), needs a clear identification of such sites to preserve them from human disturbance.

The Bay of Biscay, with its numerous estuaries and important continental shelf, stands as a high productivity area and is therefore subject to high fishing pressure. It has been studied for several decades and scientific data on fish abundance are largely available. Previous studies, e.g. Le Pape et al. (2003b), provided maps of density index over the Bay of Biscay and clearly identified essential habitats of one species: *Solea solea*. Because of high frequency and abundance of the common Sole in the Bay of Biscay compared to other demersal species (Koutsikopoulos et al., 1995) and also a regular exploitation (Anon., 2003), sole has been the only species to be considered in many previous works and thus a need for multi-specific studies is rising.

The first objective of this study is to extend the knowledge of fish essential habitats to other estuarine and costal dependent species using physical parameters known to influence fish spatial repartition and density: bathymetry (Gibson, 1997), type of sediment (Gibson and Robb, 2000) and estuarine influence (Le Pape et al., 2003b). Seven species of fishing interest have been selected for the study, all known to be common in the Bay of Biscay (Quéro, 1989). This analysis is based on young of the year fish (0-group) on which data have been gathered from surveys conducted over a 30-y period throughout the Bay of Biscay. The second objective of this study is to test another parameter, wave height, as a proxy for coastal exposure which has been evocated in Le Pape et al. 2003b as a plausible explanatory variable of juvenile fish habitat suitability.

Achievement of these two objectives relies on quantitative mapping based on the relation between 0-group densities and physical descriptors to identify nursery grounds of major importance. Generalized Linear Models (GLM) and Geographic Information System (GIS) software were combined to provide such identification and relative contributions of the different habitats have been assessed, while accounting for interannual variability of abundance and habitat extents.

2. Material and Methods

2.1. Global approach

The approach used to obtain density maps for 0-group fish is summarized in Fig. 1:

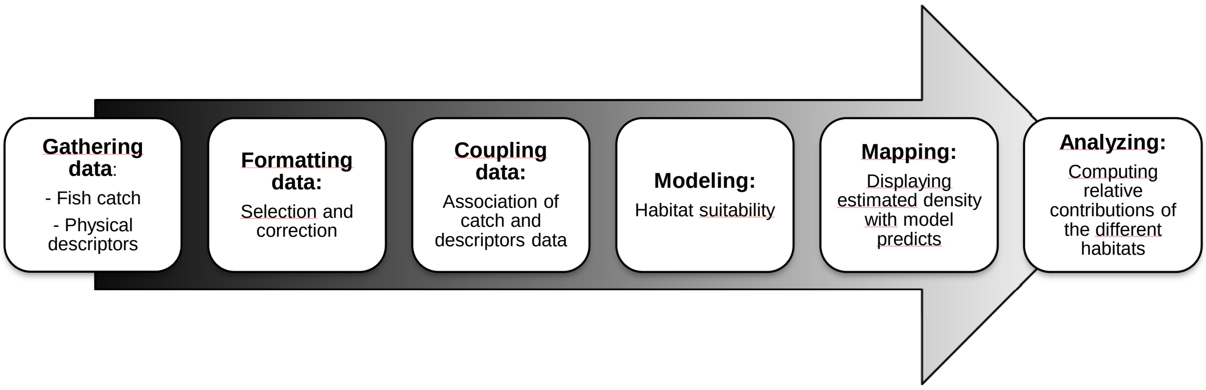

Fig. 1: Illustration of the strategy applied in this study.

2.2. Fish survey data

2.2.1. Gathering data concerning fish catch: scientific surveys in the Bay of Biscay

The study area (Fig.2) includes six major nurseries which have been delimited and treated as independent sectors due to their coastal morphology: Vilaine, Loire and Gironde that are three estuaries, Bourgneuf, the Pertuis Breton and Pertuis d'Antioche that are three bays. As this study focuses on marine species and their relation to coastal and estuarine nursery grounds, the study area was restricted to the downstream limit of the oligohaline zone within rivers and the off-shore limit was chosen to be the 36-m deep isobath.

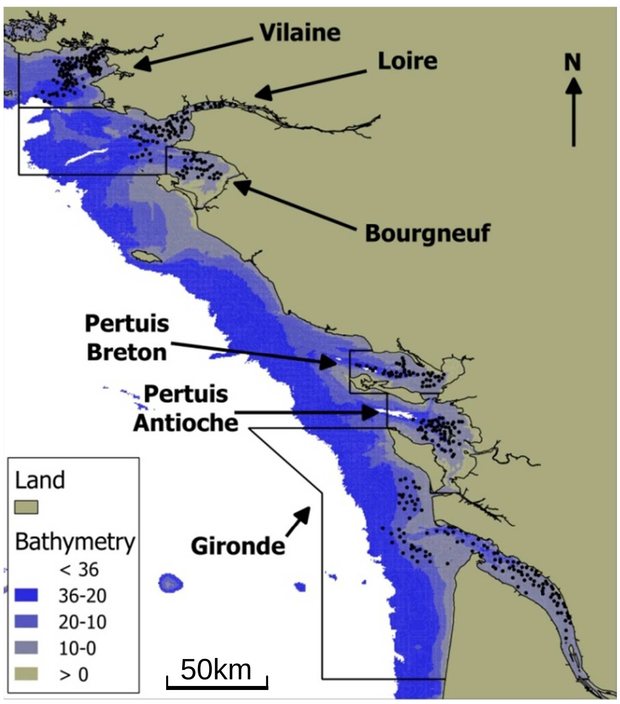

Fig. 2: Map of the study area showing the six investigated sectors and trawl hauls locations (dots).

Seven species commonly found in the Bay of Biscay (Guérault et al., 1996) were selected for this study: three benthic flatfish (*Solea solea*, *Pleuronectes platessa*, *Dicologlossa cuneata*) and four demersal round fish (*Chelidonichthys lucernus*, *Mullus surmuletus*, *Merlangius merlangus*, *Trisopterus luscus*).

Data from all available beam trawl surveys conducted throughout the Bay of Biscay from the 80s up to present have been gathered (Tab. 1). Data from three different organizations using the same gear have been retained and combined to establish an adapted dataset:

- The French Research Institute for Exploration of the Sea (IFREMER), upgrade of the data used in Le Pape et al. (2003b)
- The National Research Institute of Science and Technology for Environment and Agriculture (IRSTEA), data collected in the context of the European Water Framework Directive (Delpech et al., 2010)
- The BIO-LITTORAL scientific consultancy (BL).

As data come from three different databases it had to be standardized in order to obtain combinable data.

Table 1: Source, amount and period of the data sorted by sector

Sector	Origin of data	Hauls number	Investigation period
Vilaine	IFREMER	728	1984-1990; 1992; 1993; 1996; 1997; 2000-2005; 2008-2010
	IRSTEA	12	2009; 2010
Loire	IFREMER	214	1980; 1982-1984; 1986; 1997; 2000-2003; 2008; 2010
	IRSTEA	11	2010
	BL	15	2008
Bourgneuf	IFREMER	98	1981; 1982; 1997; 2000-2003; 2008
Pertuis Breton	IFREMER	140	1986; 1987; 1996; 2000-2003
Pertuis d'Antioche	IFREMER	169	1986; 1987; 1996; 2000-2003
Gironde	IFREMER	191	1996; 1997; 2000-2003; 2009
	IRSTEA	65	2005; 2010; 2011
Total		1643	1980-1990; 1992; 1993; 1996; 1997; 2000-2005; 2008; 2009; 2010; 2011

2.2.2. Selecting data: selection criteria

Scientific campaigns focusing on marine fish juveniles take place from late summer to mid-autumn; this period seems appropriate to study nursery grounds (Guérault et al., 1996). Only trawl hauls performed between the end of August and mid-October were selected for the study. Among these trawl hauls, valid ones using the same protocol were retained. All selected trawl hauls were performed at an average speed of 2.5 knots during approximately 10 to 20 minutes with the same gear. It was made sure that they showed no sign of tear or important clogging after the haul. The gear used is a 3-m wide beam trawl with a 20-mm stretched mesh in the codend. Further details about the beam trawl can be found in Désaunay et al. (2002).

As the aim of this study is to assess fish essential habitats, i.e. high density nursery spots, only the catch of young of the year juveniles (0-group) was retrieved. This selection was done by choosing a maximal length (at age 0) for each species. Maximal lengths were set by studying size histograms (Fig. 3 for *Solea solea* and appendix I for other species) of the catch and comparing it to bibliography when available (Tab. 2). Mean depth at length has also been shown to identify eventual shifts in the repartition of the fish which could indicate the transition from 0-group to 1-y old fish.

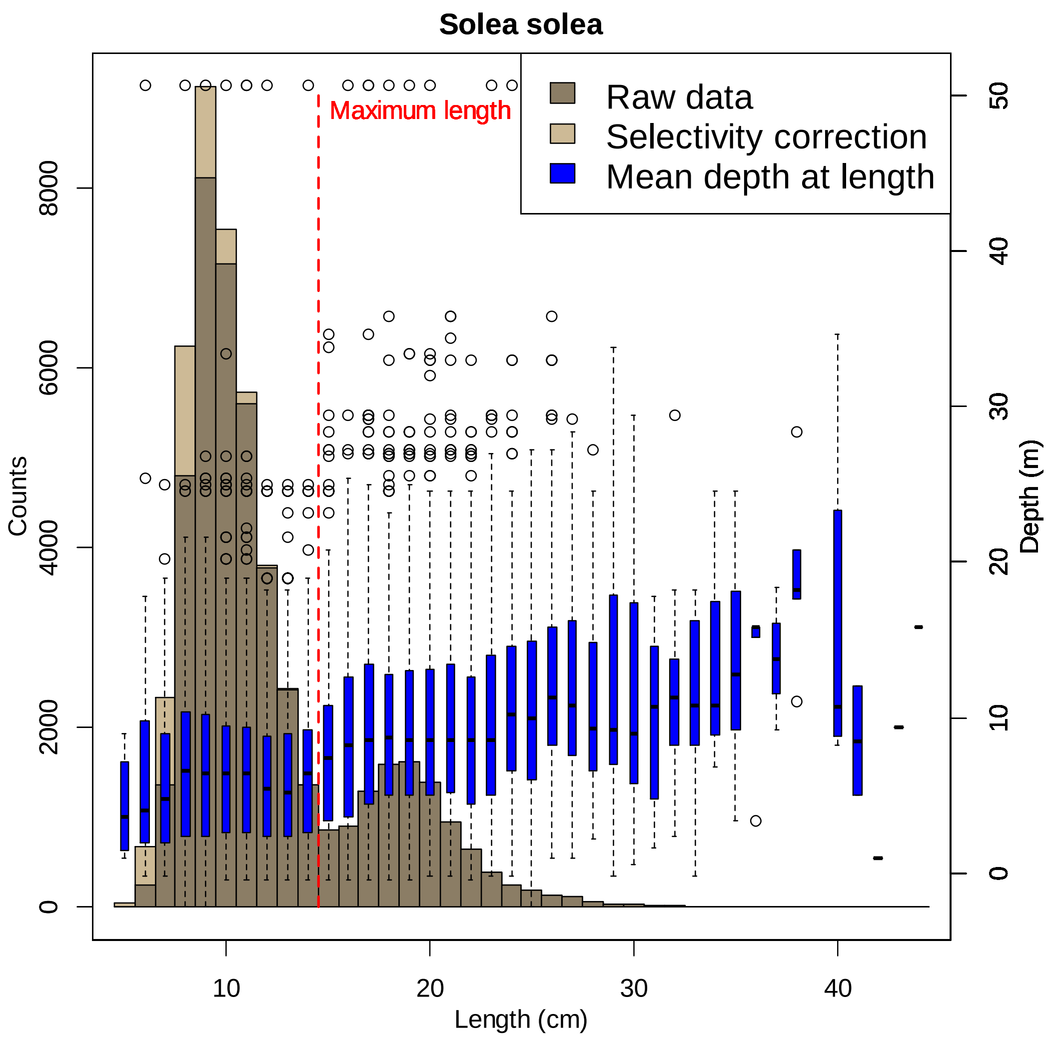

Fig. 3: Size histograms for *Solea solea* showing raw (dark shade) and corrected catch (light shade) with boxplots showing mean depth for each length class of the catch.

Table 2: Maximal length (ML) of 0-group for ***all species***

Species	ML (mm)	Source (Size histograms +)
Solea solea	150	Hermant, 2007
Pleuronectes platessa	180	Hermant, 2007
Dicologlossa cuneata	110	Hermant, 2007
Chelidonichthys lucernus	110	
Mullus surmuletus	170	N'da, 2005
Merlangius merlangus	210	Houise, 1993
Trisopterus luscus	200	Desmarchelier, 1986

2.2.3. Correcting the data: use of a selectivity factor

The catch in number of fish from 0-group was computed for each 1-cm size class on each trawl haul from the selected data. A selectivity factor has been used to correct the catch of 0-group fish which are subject to an escape phenomenon due to their small size. The estimated amount of juveniles at length L for the species s, $N_{est,s}(L)$, is given by:

$$Eq. 1: \qquad N_{est,s}(L) = \frac{N_{caught,s}(L)}{S_s(L)}$$

where $N_{caught,s}(L)$ is the actual catch of juveniles of length L, in mm, for the species s and $S_s(L)$ is the theoretic proportion of juveniles of length L and species s caught with the beam trawl. Calculation of $S_s(L)$ is based on Riou (1999) and Dardignac and de Verdelhan (1978) adapted from Rochette et al. 2010:

$$Eq. 2: \qquad S_s(L) = \frac{\exp\left[\left(\frac{2 \times L50_M \times log3}{\Delta_M}\right) \times \left(\frac{L}{L50_M} - 1\right)\right]}{1 + \exp\left[\left(\frac{2 \times L50_M \times log3}{\Delta_M}\right) \times \left(\frac{L}{L50_M} - 1\right)\right]}$$

where L is the length, in mm, M the stretched mesh size in mm, $L50_M = \alpha \cdot M$ the 50% retention length and $\Delta_M = \beta \cdot L50_M$ the selectivity range, i.e. the difference between 75% and 25% retentions lengths. According to the global shape of fishes the α parameter of *Merluccius merluccius* has been used for *Merlangius merlangus*, *Mullus surmuletus, Chelidonichthys lucernus* and *Trisopterus luscus* and the one of *Solea solea* for *Dicologlossa cuneata*. As in Rochette et al. (2010), β parameter is considered common for all species. Selectivity parameters and their associated sources are shown in Tab. 3. Resulting selectivity curves are shown in Fig. 4.

Table 3: Selectivity parameters for catch correction

Selection factor - α	Selection range ratio - β	Mesh size (mm)	Species
3,3*	0,385**	20	*Solea solea* *Dicologlossa cuneata*
2,3*	0,385**	20	*Pleuronectes platessa*
3,6**	0,385**	20	*Chelidonichthys lucernus* *Mullus surmuletus* *Merlangius merlangus* *Trisopterus luscus*

Sources: * Riou, 1999
** Dardignac and de Verdelhan, 1978

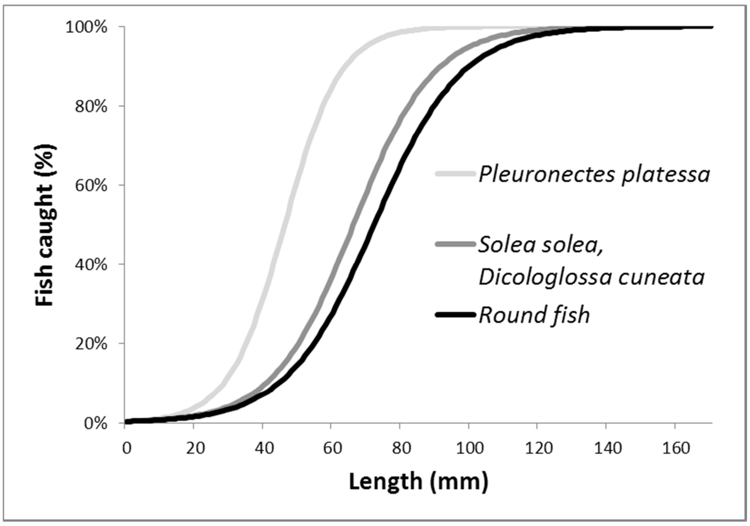

Fig. 4: Sigmoid selectivity curves resulting in percentage of fish retained (100 % corresponds to maximal capture level of the gear and not to the capture of all fish present on the trawl haul).

Selectivity correction providing corrected catch for 0-group, density has then been computed for all species on each trawl haul by summing corrected catch divided by the surface of the haul:

$$Density = \frac{\sum \frac{N_{caught,s}(L)}{S_s(L)}}{Surface}$$

Trawl hauls identified by their computed densities, locations and year of implementation were then stored as a table in a database. As the catchability of the gear is unknown, we can only estimate a number of fish which would be caught by the same gear. Thus the computing of density only provides valuable information on the relative abundance and not the absolute one.

2.3. Gathering, selecting and formatting information on physical descriptors

Data on physical parameters known to influence the repartition of coastal and estuarine nursery dependent species, i.e. bathymetry, sediment and estuarine plume (Le Pape et al., 2003b) have been gathered. Data on wave height have also been gathered to describe coastal exposure which is suspected to play an important role for such species (Le Pape et al., 2003b). Data exhaustively available over the study area have been extracted from the following sources:

2.3.1. Bathymetry

A bathymetry map, with 463-m grid sides. The bathymetric metadata and Digital Terrain Model data products have been derived from the EMODNet Hydrography portal (http://www.emodnet-hydrography.eu). Bathymetry data have been cut into 4 classes inspired from Le Pape et al. (2003b):] -36m ; -20m],] -20m ; -10m],] -10m ; -5m] and > -5m.

2.3.2. Sediment

A sediment map which is a combination of two maps of sediments in the Bay of Biscay (Lesueur, Shom). Five types of sediments are shown: Mud, fine sand, coarse sand, gravels and rocks. No trawl hauls have been realized on the latter sediment type and for modeling matters gravels and coarse sand have been gathered in one type entitled coarse sand. Additional information on sediment was needed in the Loire River and has been kindly provided by the Public Interest Group for Loire Estuary.

2.3.3. Salinity

A 3D hydrodynamic model - ECOMARS 3D (Lazure, 2009) – has been set up over the Bay of Biscay (Huret et al. 2010) providing surface salinity defined in psu from 1972 to 2008 every 6 hours. An upgrade was available including years up to 2011 thus covering the whole period of the scientific surveys. The model has a 4km horizontal regular grid and 32 vertical layers. Salinity data from the model are extracted from the surface layer and have been averaged over the first four months of each year (January to April) on each grid mesh. This variable is used as a proxy of estuarine influence which depends on the river flows. This period has been chosen regarding its important contribution to environmental enrichment and its relation to the repartition of juvenile fish (Le Pape et al., 2003a). High precipitations during this period lead to high river flows and an important input of nutrients in estuaries. In the model, salinity is cut into three classes: < 30,] 30 ; 32] and > 32, which respectively correspond to estuarine waters, mixing zone and marine waters.

2.3.4. Coastal exposure

Data from the pre-operational system PREVIMER have been requested (http://www.previmer.org/en/produits) providing wave height in meter from 2002 to 2011 on a 2km horizontal regular grid covering the whole study area. Preliminary study revealed interannual variability to be low and surpassed by spatial variability among sectors (Fig. 5). Thus wave height has been averaged over the 10-y period and used as a proxy for coastal exposure which was supposed to be a source of meso-scale variability in flatfish repartition (Le Pape et al., 2003b). The period selected for averaging wave height (May to August) was chosen for its overlay with the summer juvenile growth. Averaged wave height was then cut into four classes: < 0.3,] 0.3 ; 0.5] and > 0.5 which respectively correspond to sheltered, disturbed and agitated waters.

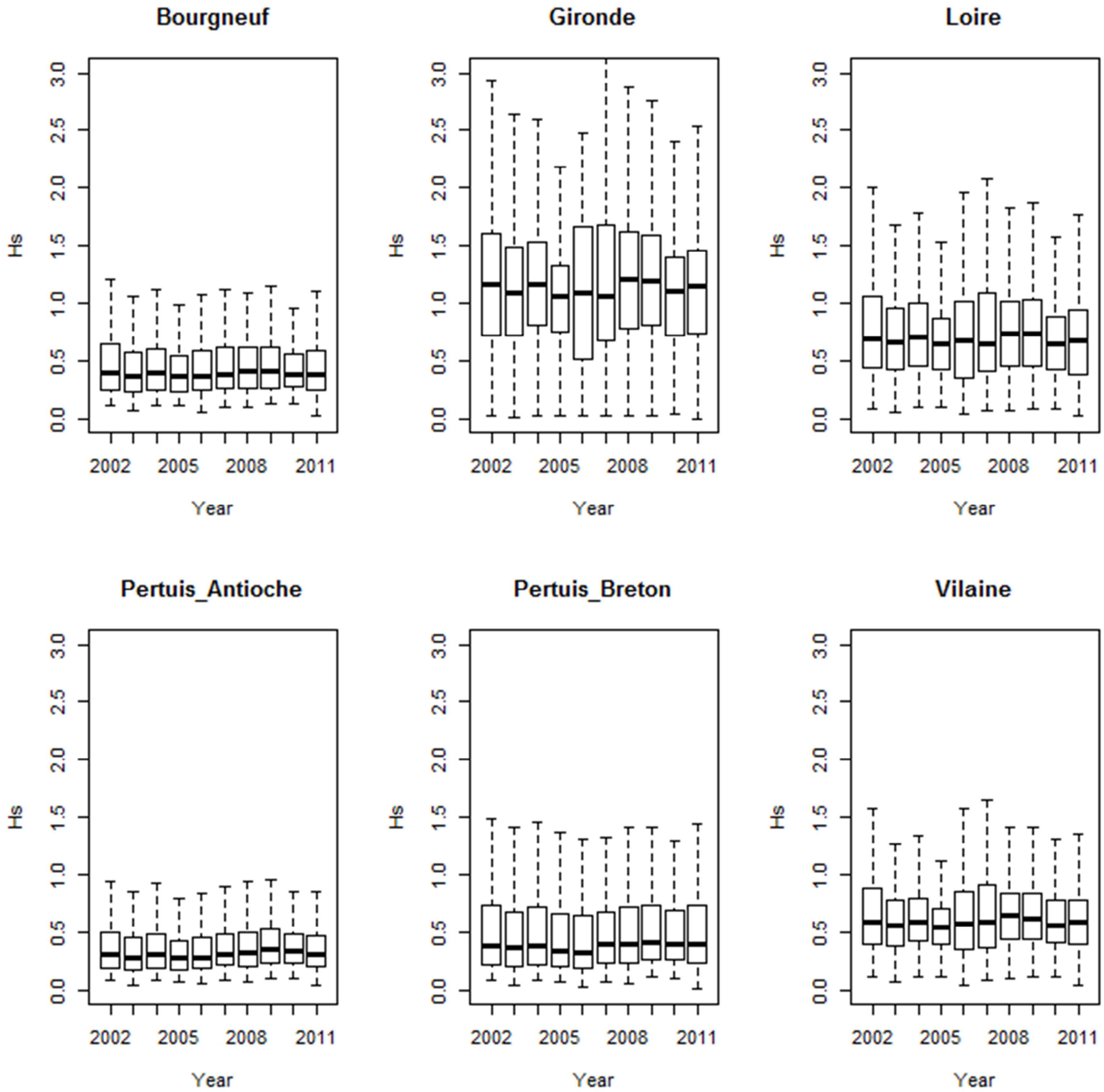

Fig. 5: Interannual variability of mean wave height (Hs) in m among the investigated sectors.

Salinity, wave and bathymetry data were inserted into a PostgreSQL database and vectorized using the resolution of their respective grids to create homogeneous polygons. Sediment data from the two sources, originally in shapefile format, were inserted into the same database and combined into a unique geo-referenced table. Sector limits (Fig. 1) were also inserted into the database and stored as a geo-referenced table. Finally, the latitude and longitude of densities where also turned into a geometry object to interact with the physical parameters.

2.4. Coupling data with physical descriptors

The location of each trawl haul was intersected with each physical descriptor and sector information. This method allowed associating values of physical descriptors and sector to the computed densities. The final dataset consists in all selected trawl hauls, their identification number, the year of implementation, the computed densities for all selected species, the local values of physical descriptors and sector. It is of importance to notice that only salinity is temporized and other physical descriptors are temporally constant. The intersection method is illustrated in Fig. 6.a.

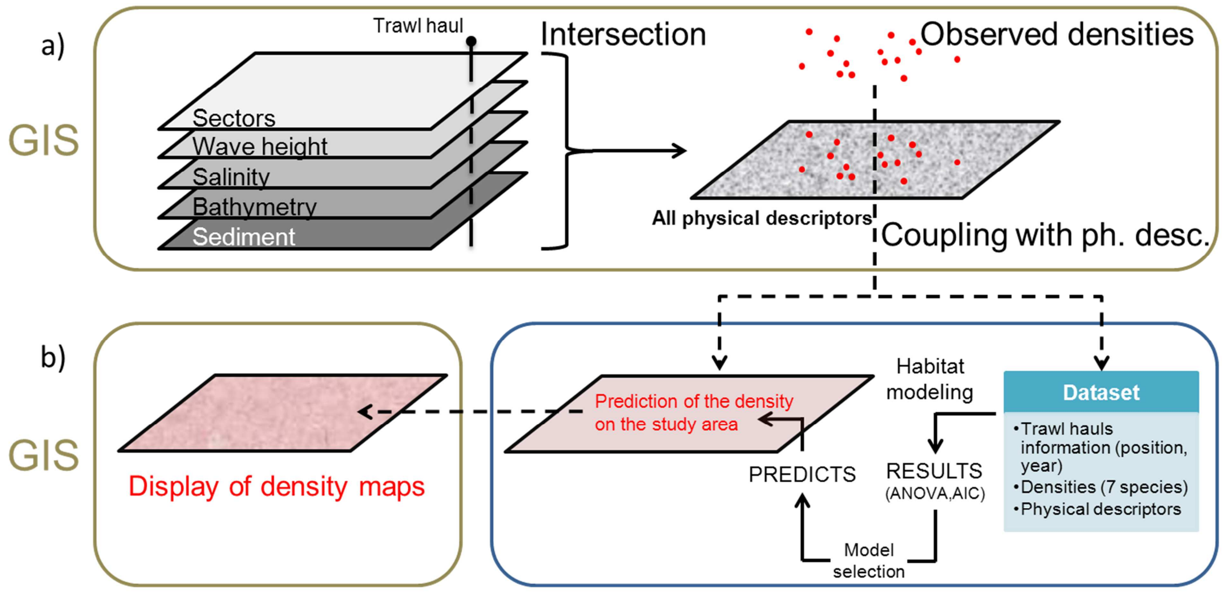

Fig. 6: Intersection method (a) to associate densities to spatial descriptors, modeling and mapping process (b). GIS is the abbreviation for Geographic Information System.

2.5. Modeling habitat suitability: the delta approach

2.5.1. Model fitting

Habitat models were built according to a delta distribution. A Binomial distribution model on the presence of 0-group has been combined with a log-normal distribution of 0-group density when present. Fitting of the two models was done separately on the two parts, relying on the maximum likelihood estimation (Stefánsson, 1996). Six parameters have been tested: the four main physical descriptors as well as year and geographic sector.

The first step of delta modeling is the Binomial modeling of presence/absence information. With $Y_{0/1,s}$ the Boolean value of juvenile presence for the species s (1 when at least one juvenile of the species s was caught, 0 otherwise) i.e. the response variable, the model is written:

$$Eq.3: \quad Y_{0/1,s} \approx F_{Salinity} + F_{Sediment} + F_{Bathymetry} + F_{Wave} + F_{Sector} + F_{Year} + \varepsilon_{0/1,s}$$

where F_{Factor} is the explanatory variable of the factor concerned and $\varepsilon_{0/1,s}$ the residuals that are assumed to be Binomially distributed. In the Binomial models, the logit link function is used.

Then a log-normal distribution is adjusted on positive density of juveniles and the model is written:

$$Eq.4: \quad \ln(Y_{+,s}) \approx F_{Salinity} + F_{Sediment} + F_{Bathymetry} + F_{Wave} + F_{Sector} + F_{Year} + \varepsilon_{+,s}$$

where $Y_{+,s}$ is the positive density of 0-group fish for the species s. The response variable is the logarithm of this latter and this GLM is fitted to a Gaussian distribution with an identity link.

Habitat suitability can then be estimated by linking the two sub-models. The estimation of the density is given by the following equation:

$$Eq.5: \qquad \hat{Y}_s = \hat{Y}_{0/1,s} \times e^{\widehat{ln}(Y_{+,s})} \times e^{\frac{\hat{\sigma}^2(\ln(Y_{+,s}))}{2}}$$

where $\hat{Y}_s$ is the estimated density for the species s, $\hat{Y}_{0/1,s}$ is the estimated probability of presence obtained from the predicts of the Binomial model and $\widehat{ln}(Y_{+,s})$ is the estimated logarithm of the density obtained from the predicts of the Gaussian model. As the Gaussian model is based on log-transformed data, the correction of Laurent (1963) has been applied. It stands as the multiplication factor $e^{\frac{\hat{\sigma}^2(\ln(Y_{+,s}))}{2}}$, where σ^2 is the standard deviation of the residuals from the Gaussian model on log-transformed densities. As the variance of the residuals could differ between the factors and classes, the correction of Laurent is necessary to obtain unbiased comparable density estimations.

Simple and cross-over effects have been tested to find the best model for every species. Chi-square tests have been run for significance and the 5 % threshold for type 1 error has been chosen as the significance limit for an effect to be retained in a model. The selection has also been based on the Akaike Information Criterion (AIC) which is an indicator of the compromise between goodness of fit and parsimony.

Consisting in two sub-models, the delta method is not adapted for the assessment of mean effects from fitted parameters in GLMs. Indeed the combined effects on a Binomial distribution and on positive log-transformed data cannot be directly interpreted. The computation of the estimated density obtained from Eq. 5 solves this problem. Mean effects have been therefore computed for each class of factor. Predicts have been generated from the models on the modeling datasets to obtain estimation of the density for each trawl haul. Mean effect of class “x” is the mean of all estimated densities on trawl hauls belonging to the class “x” divided by the overall mean estimated density. Mean effects have been computed so to obtain relative effects. A similar method has been used in Rochette et al. (2010).

2.5.2. Validation of the models

In order to validate the method, a calibration/validation method was used on models. Datasets of each species have been split in two parts: train dataset – 75% of the data – and test dataset – 25% of the data. Selection was done with respect of the relative amount of data within the different classes of factors to avoid random selection bias. Models with all factors have been run on the train dataset and predicts have been generated from those models on the test dataset.

In order to validate the models, the goodness of fit of the models has been evaluated comparing observed versus predicted values (Piñeiro, 2008). Predictions are the model fitted values for the train dataset and the values obtained from generated predicts for the test dataset. Area Under Curve (AUC) of the Receiver Operating Characteristic (ROC) (Elith et al., 2006; Townsend Peterson et al., 2008) has been used as a proxy of the goodness of fit for presence data. AUC indicator ranges from 0 to 1, where 0.5 stands for a model which correctly predicts presence once every two predictions and 1 stands for a perfectly predicting model. The coefficient of determination, R-squared, from a regression between log densities has been used to test correlation between observed and predicted log-transformed densities. The trend of standardized deviance residuals has also been analyzed. Similar goodness of fit in the train and in the test part would support the robustness of the method.

2.6. Mapping density with model predicts

A table combining the different layers of physical descriptors was created with dedicated intersection functions. This method was used to respect the original resolution of each source of information to obtain a combined stratification all over the study area. Intersection table also included sector limits. Predicts from the models have been simulated on this table providing an estimation of the presence probability and the estimated log-transformed density for each polygon of the study area. Densities have then been computed on each polygon with Eq. 5 and displayed with qGIS software to produce maps. The whole mapping process is illustrated in Fig. 6.b. Three estuarine plume scenarii have been tested; all physical descriptors being stable over time.

- Mean estuarine plume conditions: salinity is averaged over the whole period
- Minimal estuarine plume conditions: salinity values of the year with the maximal mean salinity (computed over the study area) corresponding to minimal extension of the estuarine plume
- Maximal estuarine plume conditions: salinity values of the year with the minimal mean salinity (computed over the study area) corresponding to maximal extension of the estuarine plume

Year 1992 has been chosen for minimal estuarine plume conditions and year 2001 for maximal estuarine plume conditions. They have been respectively referred to as “dry” and “wet” conditions.

2.7. Contributions of the different habitats

As a further analysis, contributions of each class of factor have been computed from the densities obtained for mapping. The number of fish on each polygon of the mapping table has been computed as the product of the density predicted on the polygon and its area. The total contribution of a class is therefore the total amount of fish on all polygons belonging to the aforementioned class (% of the total population, Le Pape et al., 2003b).

3. Results

3.1. Preliminary results

The low presence rates (Tab. 4) argue for the use of delta models for all species with a separate treatment of zero values. With less than 2% of presence rate, *Chelidonichthys lucernus* has not been retained for habitat modeling. As no fish from 0-group has been found in Gironde sector for *Pleuronectes platessa*, this sector has been removed from habitat modeling for this species.

Table 4: Presence rate for ***all species***

Species	Presence rate (%)
Solea solea	58.1
Pleuronectes platessa	19.5
Dicologlossa cuneata	12.1
Chelidonichthys lucernus	1.9
Mullus surmuletus	42.5
Merlangius merlangus	45.6
Trisopterus luscus	49.9

All factors have been retained for every species in at least one of the two sub-models except wave height in the case of *Dicologlossa cuneata*. No cross-over effect between factors has been retained in models for the following reasons:

- Cross-over effect is not retained by stepAIC method
- Cross-over effect is not significant

- Cross-over effect does not make biological sense
- Survey data do not present all possible combination or singularities in some combinations cannot be estimated because of a lack in degree of freedom leading to numerical bias in the estimation of the cross-over effect

3.2. Validation of the models

Results from validation process are shown in Fig. 7 and Fig. 8 for *Solea solea* and are summarized in Tab. 5 for all species. Residuals from the model on train dataset are given as an example in Fig. 9 for *Solea solea*. Figures for other species can be found in appendix II.

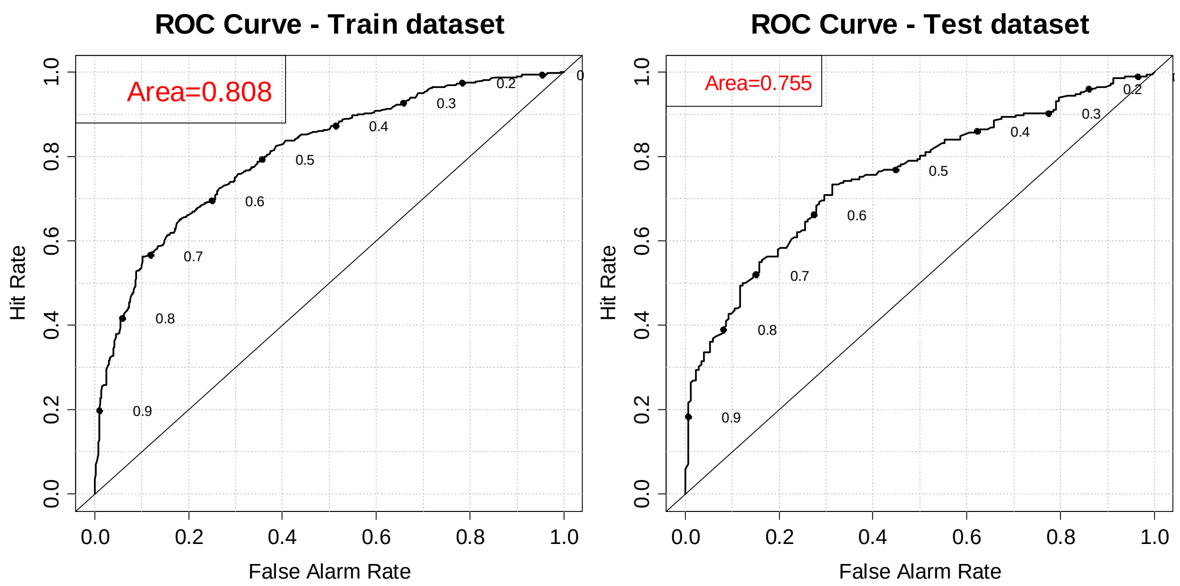

Fig. 7: ROC curve on train (left) and test data (right) for *Solea solea*. Area stands for the AUC index.

AUC indices show great prediction accuracy of Binomial models for all species. The biggest loss of the predictive capacity of the model between train and test is below 10 % (*Dicologlossa cuneata*). Prediction capacity is even better on the train dataset for *Trisopterus luscus*. As the amount of data is lower in test dataset, coefficients of determination are expected to be lower for validation data. It is the case for all species except *Merlangius merlangus*. Only *Mullus surmuletus* and *Trisopterus luscus* showed important drops between R-squared for train and test. Residuals show no particular trend in any of the selected species.

Table 5: AUC (presence data) and R² (positive densities) on train and test datasets for all species

	AUC		R^2	
Species	Train	Test	Train	Test
Solea solea	0.81	0.76	0.34	0.24
Pleuronectes platessa	0.91	0.88	0.61	0.51
Dicologlossa cuneata	0.81	0.73	0.32	0.25
Mullus surmuletus	0.80	0.77	0.29	0.09
Merlangius merlangus	0.85	0.83	0.31	0.37
Trisopterus luscus	0.82	0.83	0.37	0.16

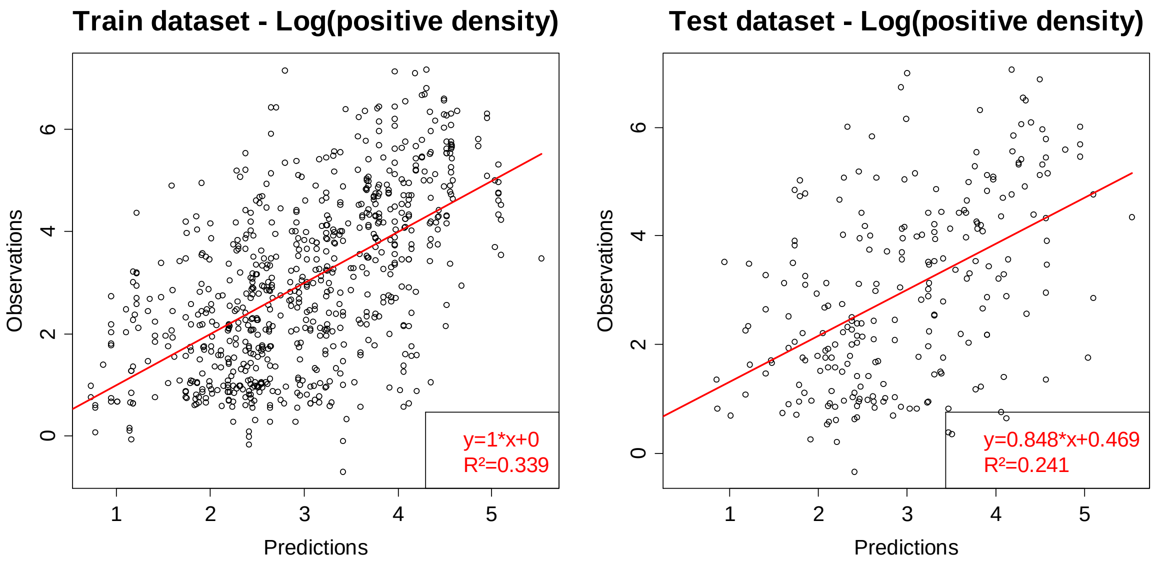

Fig. 8: Observed log-transformed densities versus predicted log-transformed densities for *Solea solea*. Fitted model values, respectively values from generated predicts, stand for predictions in the train (left), respectively test (right) data

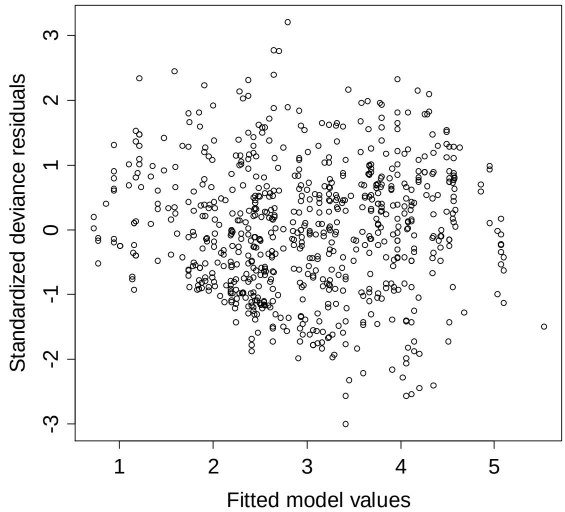

Fig. 9: Standardized deviance residuals versus fitted model values for *Solea solea* (train dataset). Fitted model values are in log scale as model is fitted on log-transformed densities

3.3. Effects of the descriptors on habitat suitability

3.3.1. The case of *Mullus surmuletus*: not enough response to physical descriptors

ANOVA results of presence and positive density are shown in Tab. 6 for *Mullus surmuletus*. Although all factors, except sector, are significantly influent on both presence and postitive density of 0-group, the percentages of explained deviance are especially low. They hardly exceed 9 % on average on the two sub-models when adding up all spatial factors. *Mullus surmuletus* can therefore not be retained for mapping process.

Table 6: Analysis of deviances for the two parts of the delta log-normal Generalized Linear Model with all factors for ***Mullus surmuletus***

Model	*AIC*	Binomial model	*1812*	Gaussian model		*2131*
	DoF*	Ex. Dev.**	Pr(Chi)	DoF*	Ex. Dev.**	Pr(Chi)
Null	0	0		0	0	
Surface salinity	2	4.1	<2.2E-16	2	3.5	2.31E-07
Sediment	2	0.6	1.22E-03	2	1.0	1.29E-02
Bathymetry	3	3.2	1.85E-15	3	1.2	1.53E-02
Mean wave	2	2.0	2.44E-10	2	0.8	3.88E-02
Geographic sector	5	1.9	5.96E-08			
Year	24	10.8	<2.2E-16	21	16.1	<2.2E-16
Total	38	22.6		30	22.6	

*DoF: Degrees of Freedom **Ex. Dev.: Explained Deviance (%)

P-values come from a χ^2-test used for significance.

3.3.2. *Merlangius merlangius* and *Trisopterus luscus*: Mismatch between area of investigation and area of repartition

Both species show better, but still low, response to the chosen physical descriptors than *Mullus surmuletus* (Tab. 7 and Tab. 8). Spatial factors explain more than 10 % of total deviance on average on the two sub-models when summing.

Table 7: Analysis of deviances for the two parts of the delta log-normal Generalized Linear Model with all factors for ***Merlangius merlangus***

Model	*AIC*	Binomial model	*1183*	Gaussian model		*1800*
	DoF*	Ex. Dev.**	Pr(Chi)	DoF*	Ex. Dev.**	Pr(Chi)
Null	0	0		0	0	
Surface salinity	2	4.9	<2.2E-16			
Sediment	2	2.6	6.50E-10	2	1.0	1.84E-02
Bathymetry	3	2.1	1.14E-07	3	5.7	1.04E-09
Mean wave	2	0.8	1.36E-03			
Geographic sector	5	3.5	2.75E-11	5	4.3	2.85E-06
Year	18	13.5	<2.2E-16	14	9.7	<2.2E-16
Total	32	27.4		24	20.8	

*DoF: Degrees of Freedom **Ex. Dev.: Explained Deviance (%)

P-values come from a χ^2-test used for significance.

Table 8: Analysis of deviances for the two parts of the delta log-normal Generalized Linear Model with all factors for ***Trisopterus luscus***

Model	*AIC*	Binomial model		*1219*	Gaussian model		*2085*
		DoF*	Ex. Dev.**	Pr(Chi)	DoF*	Ex. Dev.**	Pr(Chi)
Null		0	0		0	0	
Surface salinity		2	3.5	5.27E-13	2	1.0	1.66E-02
Sediment		2	2.5	1.04E-09			
Bathymetry		3	2.6	2.37E-09	3	3.3	5.03E-06
Mean wave		2	0.6	5.84E-03	2	1.0	1.53E-02
Geographic sector		5	2.6	6.67E-08	5	3.8	8.05E-06
Year		17	17.2	<2.2E-16	14	23.1	<2.2E-16
Total		31	29.0		26	32.2	

*DoF: Degrees of Freedom **Ex. Dev.: Explained Deviance (%)
P-values come from a χ^2-test used for significance.

Merlangius merlangus and *Trisopterus luscus* both showed strong predilection for deeper area of investigation, as bathymetry mean effects show it (Fig. 10). The area of investigation clearly does not match the area of repartition of these two species which must expend further off the 36-m deep isobath. Indeed, the estimated 0-group density increases as the bathymetry class becomes deeper. Mapping would therefore lead to a misrepresentation of the nursery habitat for these two species and thus they have not been retained for mapping process.

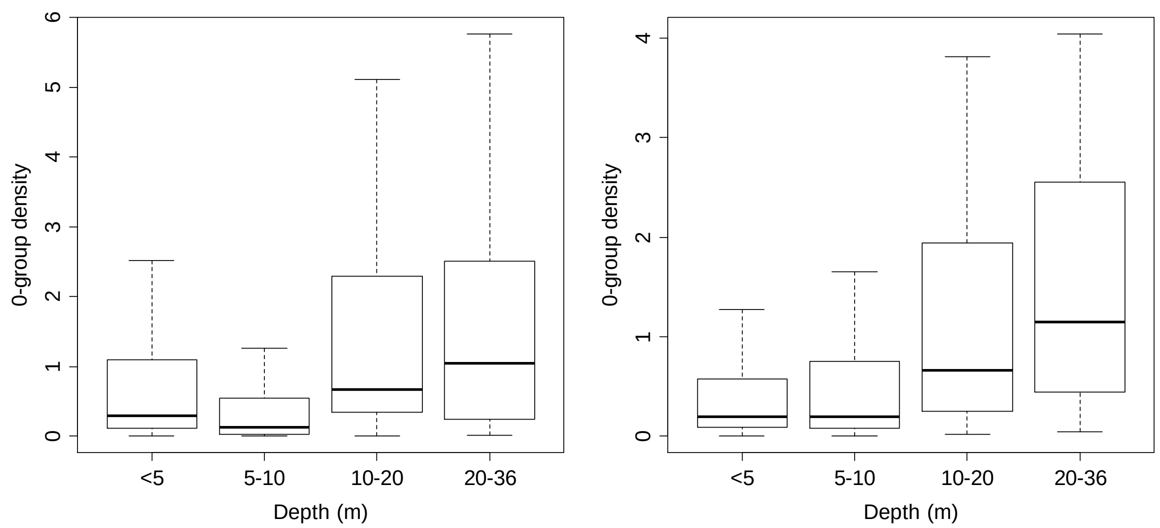

Fig. 10: Bathymetry mean effects for *Merlangius merlangus* (left) and *Trisopterus luscus* (right)

3.3.3. Flatfish

ANOVA results of the complete delta models are shown in Tab. 9 for *Solea solea* (top), *Pleuronectes platessa* (middle) and *Dicologlossa cuneata* (bottom). Mean effects of all factors are summarized in Fig. 11 for all species.

Table 9: Analysis of deviances for the two parts of the delta log-normal Generalized Linear Model with all factors for ***Solea solea*** (top), ***Pleuronectes platessa*** (middle) and ***Dicologlossa cuneata*** (bottom).

Model	*AIC*	Binomial model	*1836*	Gaussian model		*3410*
	DoF*	Ex. Dev.**	Pr(Chi)	DoF*	Ex. Dev.**	Pr(Chi)
Null	0	0		0	0	
Surface salinity	2	1.1	6.57E-06	2	3.9	3.08E-12
Sediment	2	3.2	3.91E-16	2	1.8	5.34E-06
Bathymetry	3	7.7	<2.2E-16	3	8.2	<2.2E-16
Mean wave	2	1.6	1.58E-08	2	2.8	8.89E-09
Geographic sector	5	3.1	1.81E-13	5	4.7	2.62E-12
Year	24	4.7	4.49E-12	24	10.6	<2.2E-16
Total	38	21.3		38	32.0	

Model	*AIC*	Binomial model	*820*	Gaussian model		*775*
	DoF*	Ex. Dev.**	Pr(Chi)	DoF*	Ex. Dev.**	Pr(Chi)
Null	0	0		0	0	
Surface salinity	2	4.7	1.16E-14	2	2.9	1.84E-04
Sediment	2	3.8	3.93E-12	2	6.2	1.24E-08
Bathymetry	3	15.3	<2.2E-16	3	13.1	<2.2E-16
Mean wave				2	8.1	3.65E-11
Geographic sector	4	7.4	<2.2E-16	4	4.4	3.27E-05
Year	23	13.9	<2.2E-16	21	25.4	<2.2E-16
Total	34	45.1		34	60.2	

Model	*AIC*	Binomial model	*1019*	Gaussian model		*677*
	DoF*	Ex. Dev.**	Pr(Chi)	DoF*	Ex. Dev.**	Pr(Chi)
Null	0	0		0	0	
Surface salinity	2	1.5	1.42E-04	2	5.6	9.36E-04
Sediment	2	2.1	2.94E-06	2	4.7	2.61E-03
Bathymetry	3	1.7	1.35E-04	3	4.0	1.81E-02
Mean wave						
Geographic sector	5	3.7	1.76E-08			
Year	24	13.2	<2.2E-16	23	15.9	8.46E-04
Total	36	22.1		30	30.2	

*DoF: Degrees of Freedom **Ex. Dev.: Explained Deviance (%)

P-values come from a χ^2-test used for significance.

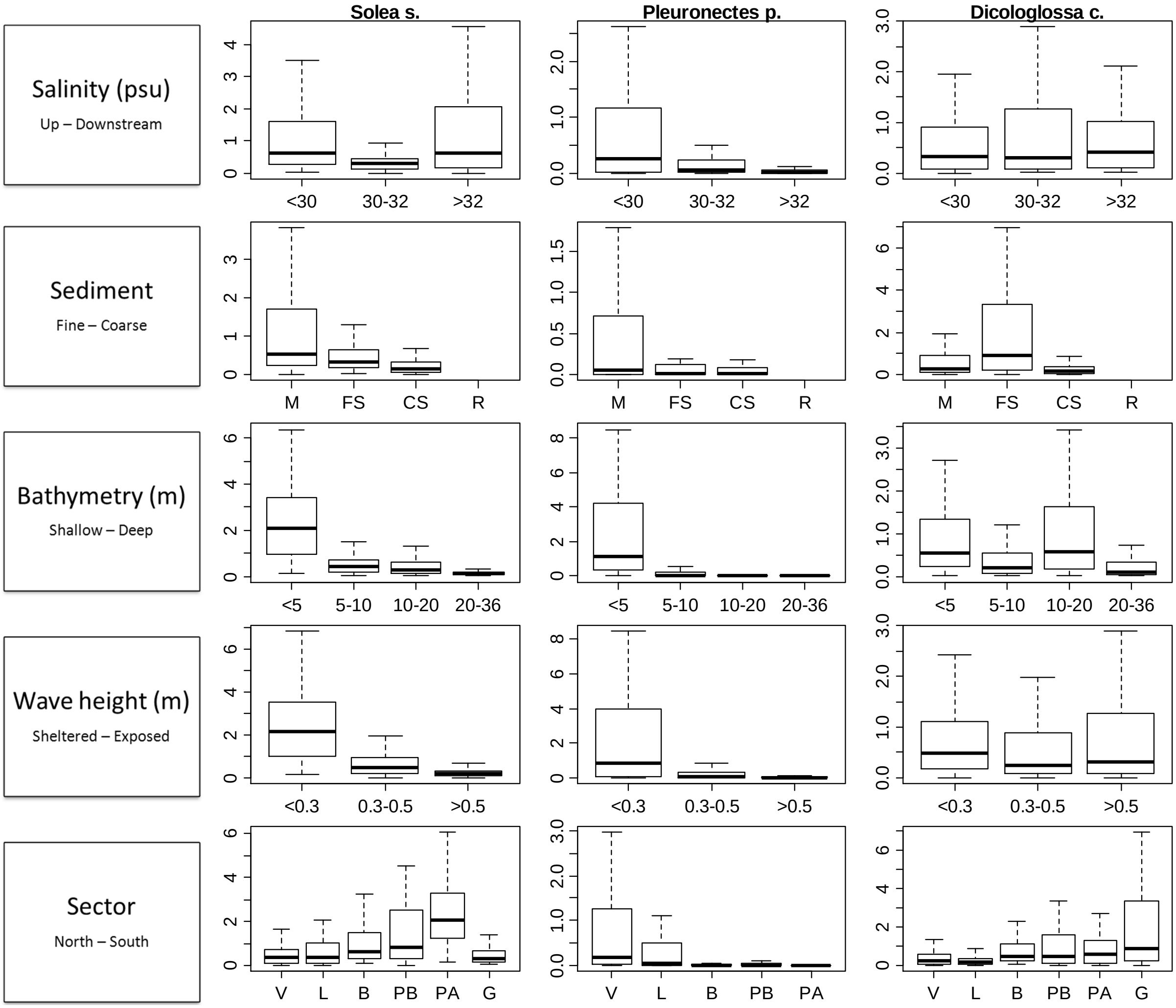

Fig. 11: Mean effects of the different factors for the three flatfish species. Factor classes are shown in x coordinate and 0-group density in y coordinate. Abbreviations for sediment: M=Mud, FS= Fine Sand, CS=Coarse Sand, R=Rock. Abbreviations for sector: V=Vilaine, L=Loire, B=Bourgneuf, PB=Pertuis Breton, PA=Pertuis d'Antioche, G=Gironde. 0-group density is in relative scale (overall mean density).

3.3.3.1. Influence of bathymetry

Bathymetry is significant for presence and positive density models of all flatfish species. This factor is a major factor for *Solea solea* and *Pleuronectes platessa* for which it respectively explains roughly 8 % and 14 % of deviance in both presence and positive density models. This factor is more influent on the presence of 0-group of these species than on its density, when present. *Dicologlossa cuneata* seems less influenced by bathymetry with respectively 1.7 % and 4 % of explained deviance in presence and positive density models. Bathymetry mean effects confirm the high influence of this factor on *Solea solea* and *Pleuronectes platessa* (Fig. 11) for which it reveals a strong predilection for shallow waters. Indeed, strong drops in the estimated density can be observed as bathymetry increases. The effect of the shallower class of bathymetry, i.e. < 5 m, is approximately four times higher than the one of the upper class (5-10 m) for both species.

3.3.3.2. Influence of sediment type and salinity

Sediment type and salinity are significant in both presence and positive density model for all flatfish species. Althought they both are of lesser influence than bathymetry, mean effects reveal some trends and dependences. *Solea solea* and *Pleuronectes platessa* both present a strong dependence to mud and *Dicologlossa cuneata* to fine sand. *Pleuronectes platessa* shows a strong dependence to estuarine waters (Fig. 11), whereas it is less obvious for the two other flatfish species.

3.3.3.3. Influence of wave height

Wave height is significant on both presence and positive density of 0-group for *Solea solea* and only on the positive density for *Pleuronectes platessa*, on which it is particularly influent. It accounts for at least half of the meso-scale variability (Geographic sector) for all flatfish species (Tab. 9). Mean effects reveal particularly strong predilections of *Solea solea* (Fig. 11) and *Pleuronectes platessa* for sheltered areas, i.e. areas belonging to the lowest wave height class (< 0.3 m). Mean effect decreases rapidly as wave height increases for both species.

3.3.3.4. Geographic sector: remaining meso-scale varibility

Geographic sector is significant on both presence and density of 0-group for all flatfish species except *Dicologlossa cuneata* for which it is only significant on presence of 0-group (Tab. 9). Sector is particularly effective to discriminate presence of *Pleuronectes platessa* and *Dicologlossa cuneata* rather than *Solea solea*. Indeed, these two flatfish have strong latitudinal trends, as shown by the mean effects (Fig. 11): a north increase for *Pleuronectes platessa* versus a north decrease for *Dicologlossa cuneata*.

3.3.3.5. Interannual variability

Year factor is significantly influencing presence and positive density of 0-group for all flatfish species. It is more significant on positive density than on presence. Interranual variability is lower than spatial variability (spatial factors) for *Solea solea* and *Pleuronectes platessa*, whereas it is the opposite for *Dicologlossa cuneata* (Tab. 9). Mean effects allow insights in the interannual variability of presence and positive density for 0-group. However, as some years are missing and all sectors were not investigated each year, results are to be taken with a particular care concerning the analysis of temporal trends and shifts. Yet it can still be interpreted as abundance indices and it reveals some disappearance and reappearance events on the studied species. *Pleuronectes platessa* and *Dicologlossa cuneata* show strong opposite trends. The previous progressively disappears from the late 1980s to the early 2000s whereas the latter progressively increases over the same period (Fig. 12).

3.4. Mapping: identification of nursery areas and relative habitat contributions

At this stage, *Merlangius merlangius* and *Trisopterus luscus* have been removed from mapping process because bathymetry effects showed that their repartition areas do not match the study area. *Mullus surmuletus* is also to be removed because the percentages of presence and density model deviances explained by the spatial factors are on average too low. Therefore, only the three flatfish species have been selected to undergo mapping process. Density maps for mean estuarine plume conditions are respectively shown in Fig. 13 for *Solea solea*, *Pleuronectes platessa* and *Dicologlossa cuneata*. Density maps for other estuarine plume conditions can be found in appendix III. Relative contributions of the different class of factor or “habitats” can be found in Tab. 10 for mean estuarine plume conditions and in appendix IV for other conditions.

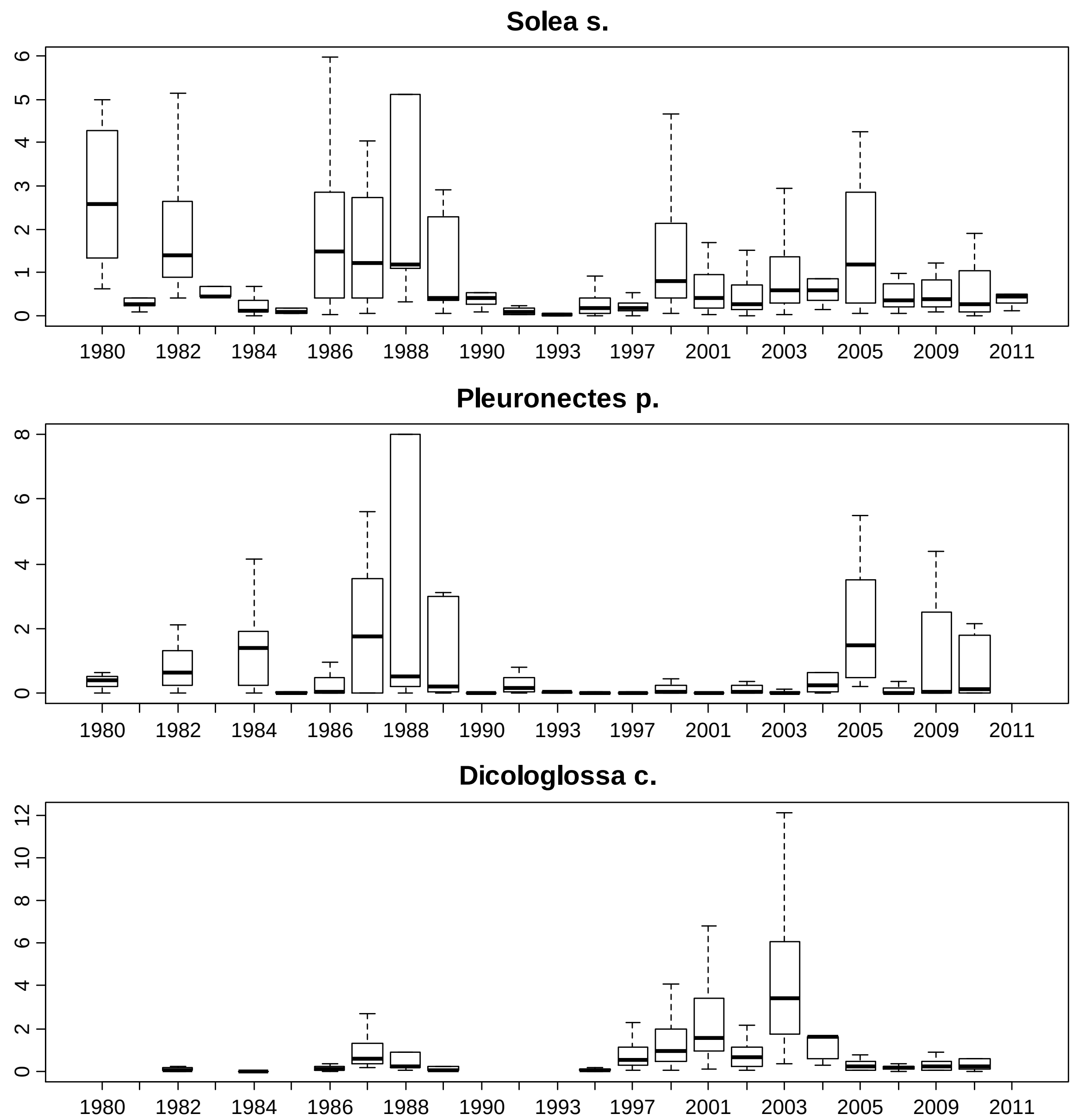

Fig. 12: Year mean effects for the three flatfish species. Factor classes are shown in x coordinate and 0-group density in y coordinate.

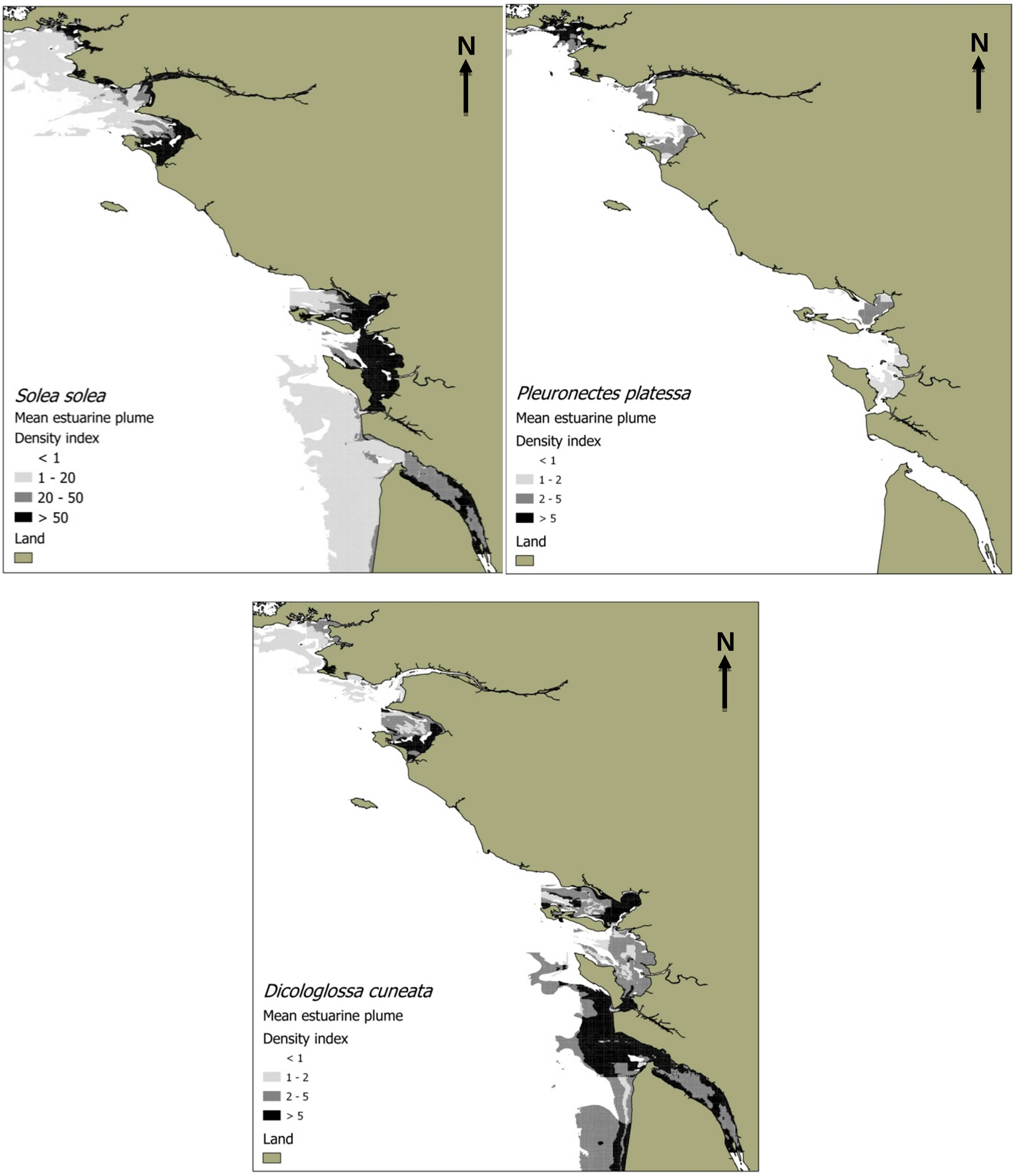

Fig. 13: Density map for *Solea solea* (top left), *Pleuronectes* platessa (top right) and *Dicologlossa* cuneata (bottom) with mean estuarine conditions.

High densities of *Solea solea* 0-group can be found on a few coastal areas, near the river mouths or in sheltered bays. The same coastal dependence can be observed for *Pleuronectes platessa* and *Dicologlossa cuneata* although indexes are considerably lower for these two species. Density index scale has been divided by 10 for a better observation of the repartition of these two species. Among the latters, repartition of *Dicologlossa cuneata* expends a little further off the coast. Variability in salinity was the main source of variability for the habitat and strongly impacts the contributions of marine, estuarine and mixing waters. It does not really impact the relative contributions of the other habitats except for *Dicologlossa cuneata*.

Table 10: Relative contribution and area by class of factor under ***mean estuarine plume*** conditions

	Conditions	Solea s.		Pleuronectes p.		Dicologlossa c.	
Factor	Class	Contr. (%)	Area (%)	Contr. (%)	Area (%)	Contr. (%)	Area (%)
Salinity	> 32	56.3	50.7	14.7	41.0	31.5	50.7
	] 30 ; 32]	24.1	28.7	38.4	39.4	34.9	28.7
	< 30	19.7	20.5	46.9	19.6	33.6	20.5
Sediment	Mud	75.5	48.2	77.7	55.6	38.7	48.2
	Fine sand	18.7	32.4	10.0	13.4	55.6	32.4
	Coarse sand	5.8	19.4	12.3	31.0	5.7	19.4
Bathymetry	> -5	77.7	23.0	80.9	35.1	37.8	23.0
	] -10 ; -5]	11.4	17.9	13.0	17.1	16.6	17.9
	] -20 ; -10]	8.1	23.3	5.7	25.5	35.2	23.3
	] -36 ; -20]	2.8	35.9	0.5	22.3	10.4	35.9
Wave height	< 0.3	67.6	18.6	44.3	22.0	31.4	18.6
	] 0.3 ; 0.5]	15.2	8.2	20.2	16.6	6.7	8.2
	> 0.5	17.2	73.1	35.4	61.3	61.9	73.1
Geographic sector	Vilaine	4.6	10.3	55.3	21.6	4.1	10.3
	Loire	6.4	15.3	16.8	32.0	1.8	15.3
	Bourgneuf	13.1	5.9	12.6	12.2	6.5	5.9
	Pertuis Breton	14.9	7.4	8.5	15.4	9.5	7.4
	Pertuis Antioche	44.2	8.9	6.8	18.7	9.4	8.9
	Gironde	16.8	52.2			68.6	52.2

Muddy areas largely contribute to the total population of 0-group fish for *Solea solea* and *Pleuronectes platessa* with contributions between 75 % and 78 % of the total 0-group population. Contribution of shallow waters is also really high for these two species with approximately 80 % of the total 0-group located in the shallowest class of bathymetry. Sheltered areas (Wave height < 3 m) contribute to two-thirds of the total 0-group population for *Solea solea* whereas only 44 % and 31 % respectively for *Pleuronectes platessa* and *Dicologlossa cuneata*. Contributions of estuarine waters vary greatly from dry to wet conditions, gathering a maximum of roughly 50 % of the total 0-group population of *Solea solea* and *Dicologlossa cuneata* during a wet year. This phenomenon is even greater for *Pleuronectes platessa* with an 85 % contribution of estuarine waters during a wet year.

4. Discussion

4.1. Relevance of the method applied

Marine fish abundance survey data are a typical case of zero inflated data, with associated high variability in the remaining positive data. The data of the present study present even more zeros due to the selection of a particular life stage (0-group). The delta method implemented in this study enables to process such zero inflated data but has limits such as the correlation between the two datasets (presence-absence and positive density datasets). Indeed, the construction of the two sub-models relies on the hypothesis according to which the probability of presence and the distribution of the positive catch are independent. Data reveal that sites with a high probability of presence are also sites harboring high densities. Presence and density can therefore not be considered as independent and the bias introduced by the calculation of the estimated density as the simple product of the two probabilities is unknown.

Alternative methods, e.g. compound Poisson process (Ancelet et al., 2010) or Tweedie distribution (Shono, 2008), have been implemented and tested. They provided similar results as the delta method and are more complicated to implement. The delta method was therefore implemented here for it was the most straightforward method to fulfill the objectives of the study. It is commonly used to process such data (Stefánsson, 1996; Welsh et al., 1996; Ye et al., 2001; Brynjarsdóttir and Stefánsson, 2004) because of its simplicity, which is its major asset. A second asset of the method is the separate analysis of the probability of presence on the one hand and the level of positive catch on the other hand. Such segregation allows a more refined analysis with different variables accounting for the two sub-models. Different ecological interpretations can therefore emerge.

A validation process implementing a train and a test dataset and comparing results, such as what has been done in this study, is however required to evaluate the robustness of the method. Such validation gives credit to the habitat model above all and secondly to the method itself. A second proof of the robustness of the method comes from the similarities observed between the results of this study and a previous one (Le Pape et al., 2003b) concerning *Solea solea*. The initial dataset was upgraded with ten years of data and furthermore upgraded with data in the inner part of rivers, which are totally new locations. Despite this tremendous change, results are particularly close and the same general trends can be highlighted. This consistency in results can therefore be considered as another proof of the robustness of the method and its appropriateness to study juvenile fish habitat suitability.

4.2. Confirmation of habitat predilections for Solea solea and generalization of these trends to coastal and estuarine dependent flatfish species

Although the coastal nursery dependence of *Solea solea* has already been demonstrated in Le Pape et al. (2003b), the present study strengthens the general trends highlighted before, for *Solea solea*, and reveals quite similar patterns concerning the other studied flatfish:

- Shallow (< 5 m) and muddy (mud) waters contribute greatly to the total population of 0-group from *Solea solea* and *Pleuronectes platessa*. These areas can therefore be considered as essential nursery habitats for these two flatfish. They harbor more than 60 % of both total populations whereas representing only 16 % of the overall study area. Besides, locations deeper than 20 m and grounds not covered with mud, or at least fine sediment for *Solea solea*, are unsuitable as nursery grounds for these two species. Dependence to shallow muddy areas is even stronger for *Pleuronectes platessa*. *Dicologlossa cuneata* does not show such strong trends but is dependent to grounds covered with fine sand for nursery. Locations deeper than 20 m are also unsuitable as nursery grounds for this species.

- Estuarine waters contributed greatly to 0-group population of *Pleuronectes platessa* and in a more modest way for *Solea solea* and *Dicologlossa cuneata*. A bottom up process through the trophic chain was preliminary evocated to explain the particularly rich benthic community in estuarine areas and thus their high potential as nursery grounds for flatfish species who feed on benthic invertebrate (Darnaude et al., 2004, Kostecki et al., 2010). This relationship between nursery grounds and rich benthic fauna has been confirmed for *Solea solea* (Nicolas et al., 2007) and is supported by the present study for *Pleuronectes platessa* and *Dicologlossa cuneata* which depend on similar locations as nursery grounds.

The three studied flatfish can all be considered as estuarine and coastal nursery dependent species although their habitat predilections slightly vary from one species to another.

4.3. Highlighting the positive effect of sheltered habitats

Preference of *Solea solea* and *Pleuronectes platessa* for sheltered areas has already been supported (Pihl and Van der Veer, 1992; Le Pape et al., 2003b) and is now brought out from quantitative approach on the negative influence of wave on habitat suitability. However, no proper parameter had ever been used to explain this link between sheltering places and high densities of 0-group fish for these two species. The addition of wave height as a proxy of coastal exposure to explain repartition of *Solea solea* and *Pleuronectes platessa* 0-group is successful. This influence explains half as much deviance as the remaining meso-scale variability. Wave height is also significant for *Pleuronectes platessa* on positive density of 0-group and explains twice as much deviance as the remaining meso-scale variability. This new descriptor has therefore to be considered as an unavoidable explanatory variable for habitat modeling on 0-group fish of these two species. Wave height have not showed significant influence on *Dicologlossa cuneata* and can therefore not be generalized to other flatfish species.

4.4. Meso-scale and interannual variability

Compared to results of Le Pape et al. (2003b) meso-scale variability has decreased considerably: 11.8 % and 20.9 % in the two models for *Solea solea* versus 3.1 % and 4.7 % now. The introduction of wave height as a physical descriptor captured a part of the deviance but it is not enough to explain the drop in meso-scale explained deviance. For *Solea solea*, the presence of two important spawning grounds off the coast in front of the main nursery grounds (Abbes, 1991 in Mahe et al. 2007) gives credit to larval supply as a plausible source of meso-scale variability. *Pleuronectes platessa* and *Dicologlossa cuneata* showed strong meso-scale variability linked to latitudinal trends, they respectively increase and decrease as latitude increases. This phenomenon can be explained by the Bay of Biscay being respectively the southern and northern limit of repartition for these two species (Désaunay et al., 2006; Hermant et al., 2010).

Among spatial factors, only salinity had a temporal dimension. Interannual variabiltiy in the models is therefore a mix of wave height interannual variability, which was verified to be lower than its spatial variability, and interannual variability of other unused factors such as larval supply and environmental parameters, e.g. temperature. Interannual variability is high for Solea solea but presents no particular trend and can therefore be interpreted as environmental noise at least partly linked to recruitment variability during larval stage before juvenile settlement on nursery grounds. In the case of *Pleuronectes platessa* and *Dicologlossa cuneata*, strong temporal trends are revealed: disappearance of *Pleuronectes platessa* from the early 1990s to the mid-2000s and progressive increase of *Dicologlossa* *cuneata* from the late 1990s. Both trends were proved to be significant (Désaunay et al., 2006) and were confirmed to come from a progressive warming of the waters in the Bay of Biscay occurring during the investigation period and impacting northern flatfish (e.g. *Pleuronectes platessa*) and southern flatfish (e.g. *Dicologlossa cuneata*) oppositely (Hermant et al., 2010).

4.5. Remaining unexplained deviance

The percentage of deviance not explained by the habitat models ranged from 40 % to 80 % among the three flatfish species. Several reasons can explain high residual deviance:

- Classification for salinity highly depended on the amount of available data and more data in the rivers would provide more refined classes. The mean salinity has a strong spatial variability and this latter should account in the identification of the estuarine plume.
- Other environmental variables, such as presence of *Crepidula fornicata* evocated in Le Pape et al. (2003b), could be considered. This invasive mollusc have a strong negative impact on the benthos and thus on the habitat of benthic fish (Sauriau et al., 1998). More information on the substrate, and especially about the benthic community, which stands as the major food source for the studied flatfish (Le Pape et al., 2007; Nicolas et al., 2007), could be better explanatory variables than the type of sediment, with only three different classes, used in this study.

4.6. A real difficulty to model habitat suitability for demersal species

The delta method implemented in this study appears to be inappropriate for the four roundfish species for various reasons:

- Data are too scarce for rare species, such as *Chelidonichthys lucernus*. The lack of information in data with a really important proportion of zero values can only be overcome with more data. Due to the important costs of scientific surveys, such an increase in data harvest is not possible and difficult to ask for species with low occurence.
- The investigation area is too limited for species with 0-group fish having a large area of repartition as for *Merlangius merlangus* and *Trisopterus luscus*. The scientific surveys focusing on nursery grounds have indeed been implemented to match the area of repartition of coastal nursery dependent species such as *Solea solea*.
- Some selected species do not respond to the physical descriptors used in this study. This is the case for *Mullus surmuletus*, *Merlangius merlangus* and *Trisopterus luscus.* For the two latter species it might be because of their weaker dependence to benthos for feeding. They indeed feed on pelagic crustaceans during 0-group phase (Quéro and Vayne, 1997) and not on benthic invertebrates. In the case of *Mullus surmuletus*, the absence of trawl hauls on rocky area could be a source of explanation. Rocky areas are excluded from study because trawling on these areas can damage the gear. *Mullus surmuletus* can be found on rocky grounds (Quéro and Vayne, 1997 in Mahe et al., 2007) and sediment type effects are consistent with this fact. The lack of observation on rocky areas could therefore be a source of explanation for the irrelevance of the model for this latter species.

New habitat descriptors have to be implemented to extend habitat modeling to species which do not follow the same habitat patterns as the known coastal and estuarine nursery dependent species. New sampling methods also need to be implemented especially for the investigation on rocky shores.

4.7. From habitat suitability to fish stock management

The sheltered areas which harbor high 0-group densities of estuarine and coastal nursery dependent flatfish species appear as priority sites to be protected for the conservation of these species. They gather a large amount of the total 0-group population in a small area and are therefore necessary to insure renewal of the fish stock (Le Pape et al., 2003b; Dahlgren et al., 2006). This method is appropriate for management in the context of ecosystem approach to fishery and provides insightful results to be used for MPA design. The protection of a few restricted essential habitats common to the three studied flatfish species appears as a top priority at the scale of the Bay of Biscay.

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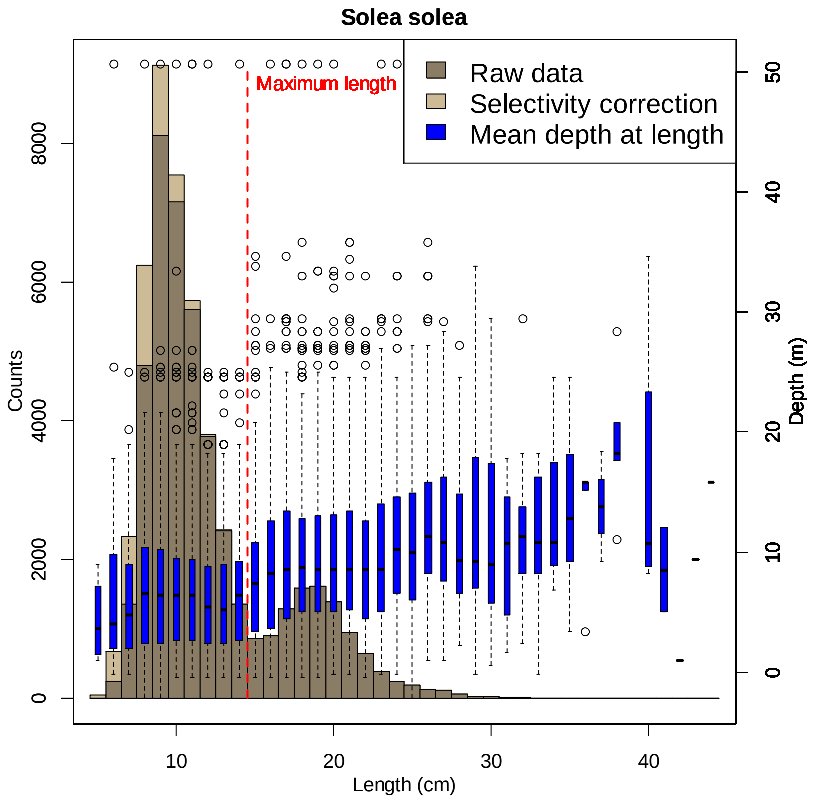
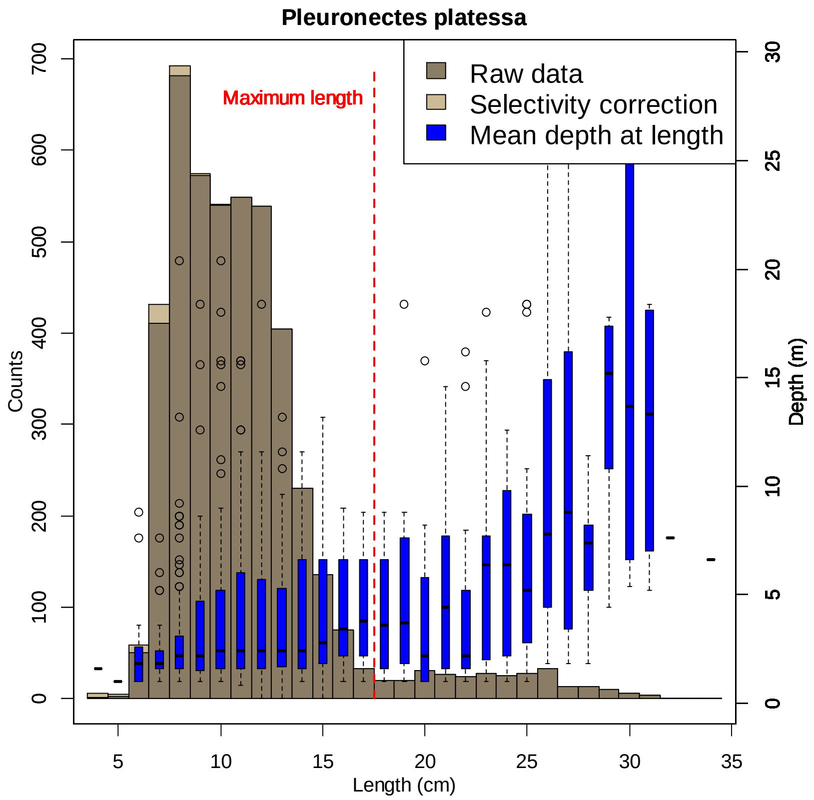
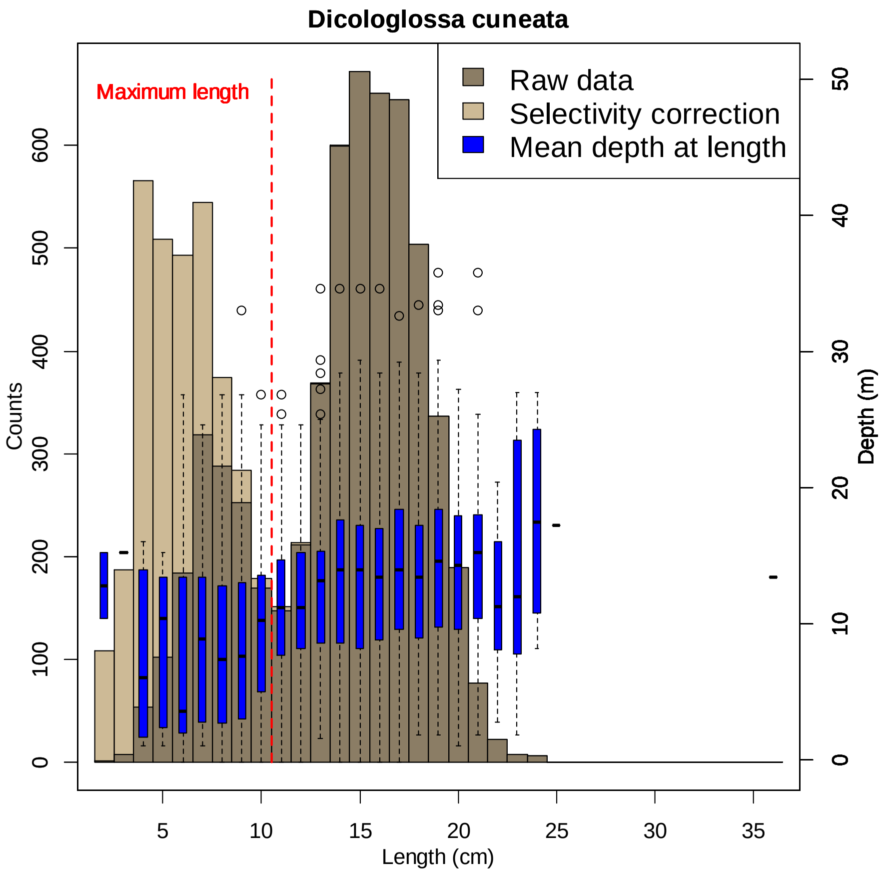
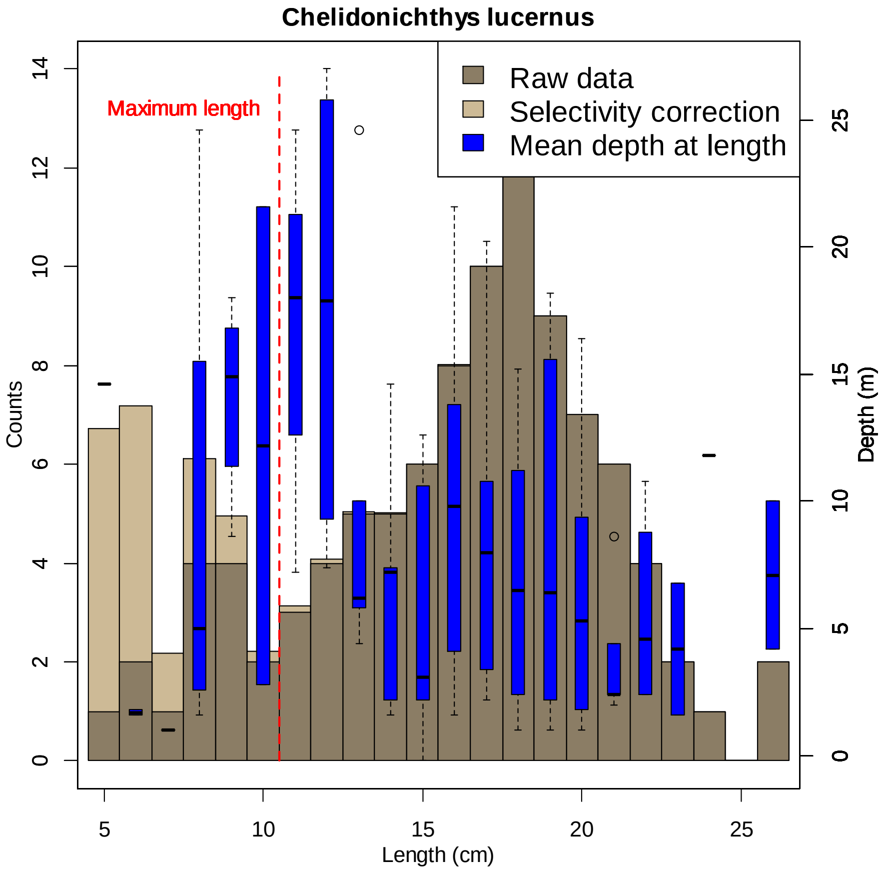
Appendix I: Size histograms



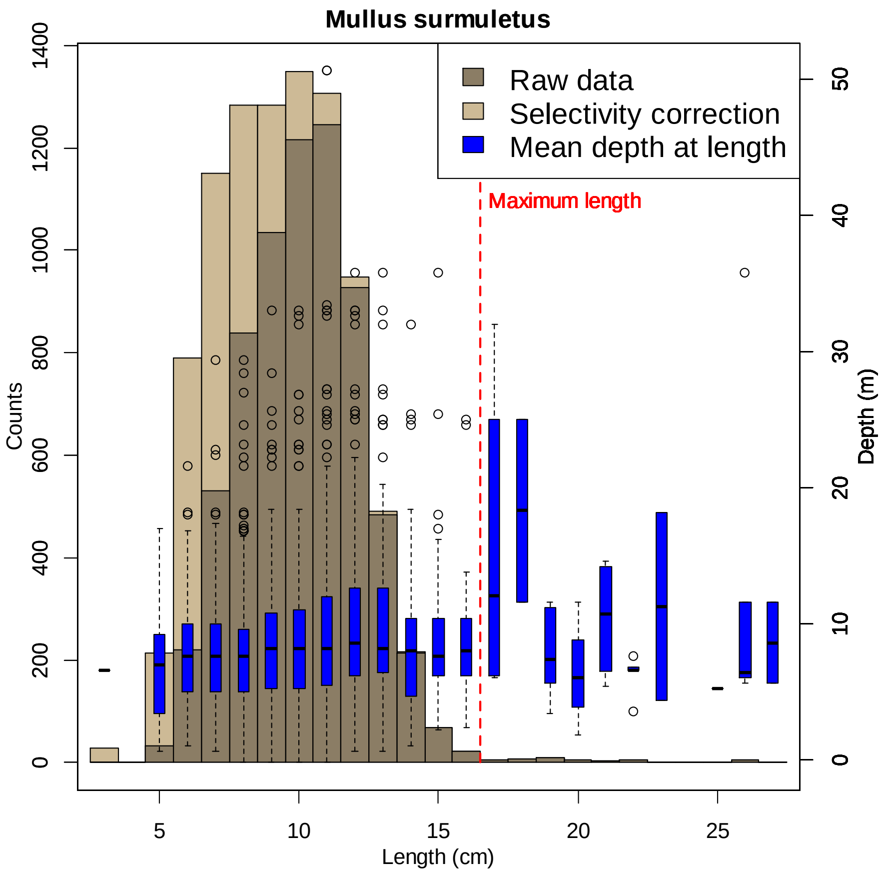




Dicologlossa cuneata
Maximum length
Raw data
Selectivity correction
Mean depth at length
Counts
Depth (m)
Length (cm)



Chelidonichthys lucernus
Maximum length
Raw data
Selectivity correction
Mean depth at length
Counts
Depth (m)
Length (cm)



Mullus surmuletus
Raw data
Selectivity correction
Mean depth at length
Maximum length
Counts
Depth (m)
Length (cm)
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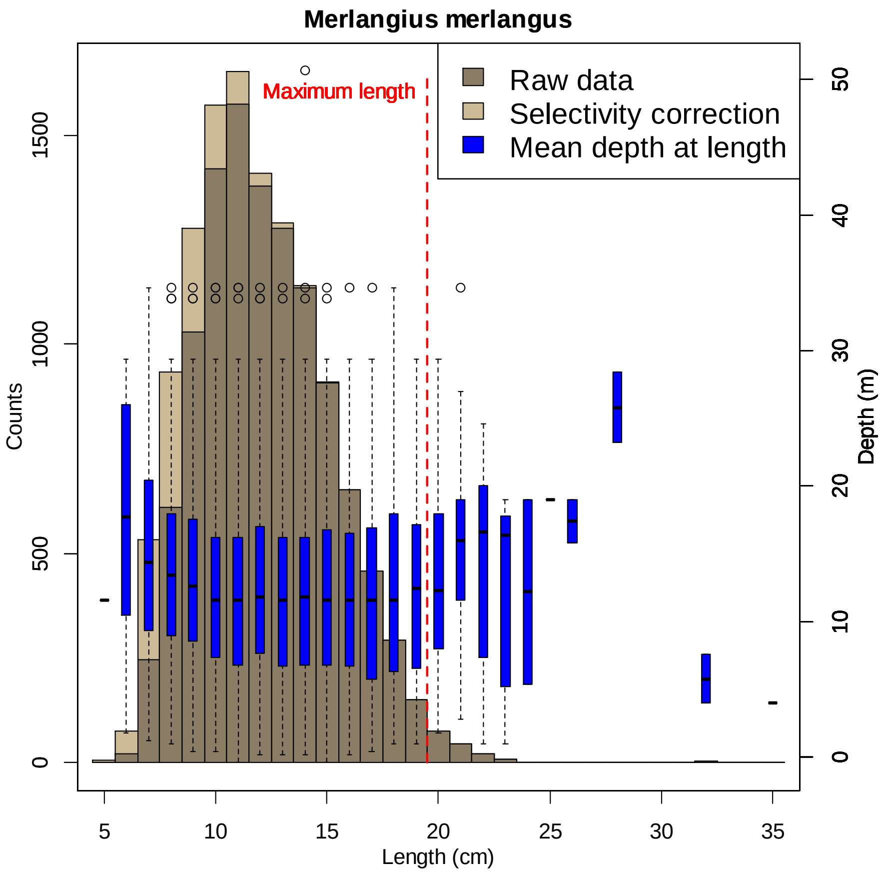
600
800
1000
1200
1400
0
10
20
30
40
50
5
10
15
20
25



Merlangius merlangus
Raw data
Selectivity correction
Mean depth at length
Maximum length
Counts
Depth (m)
Length (cm)
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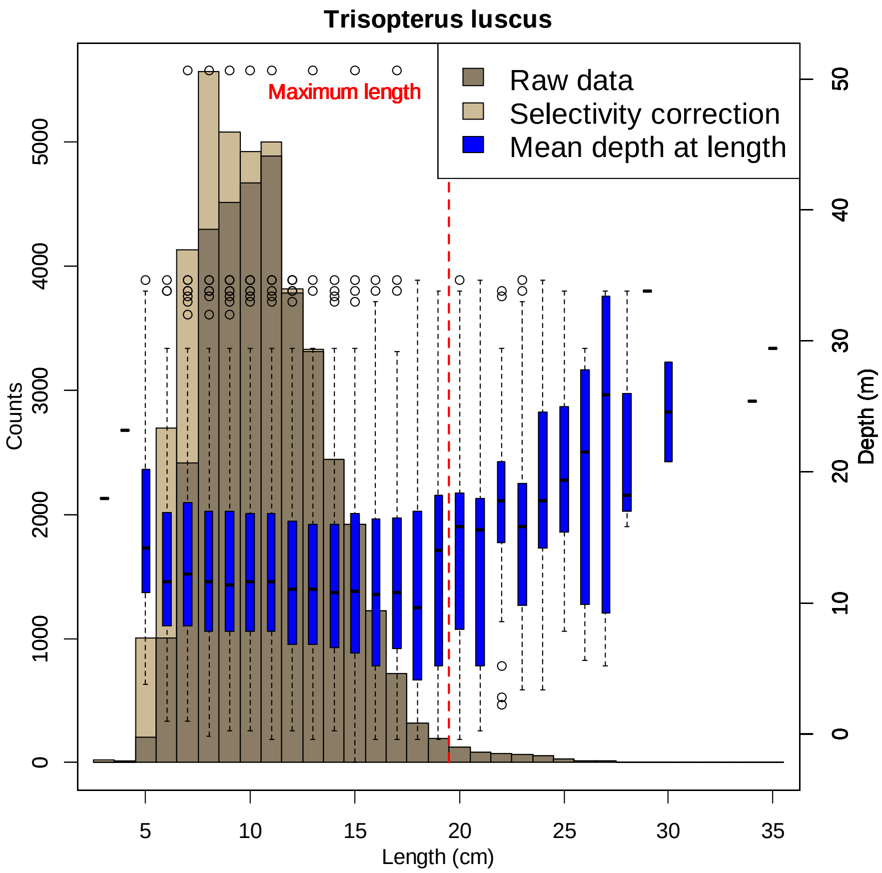
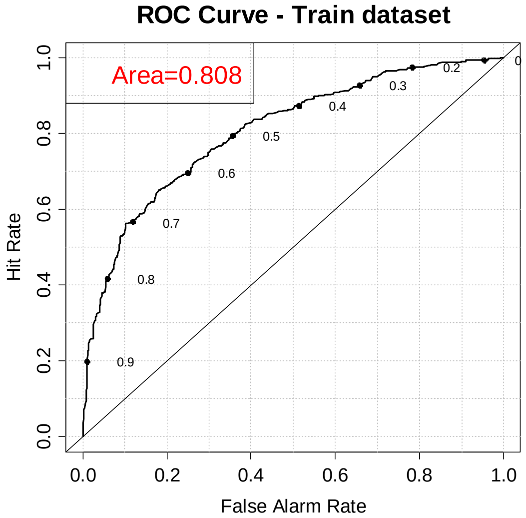
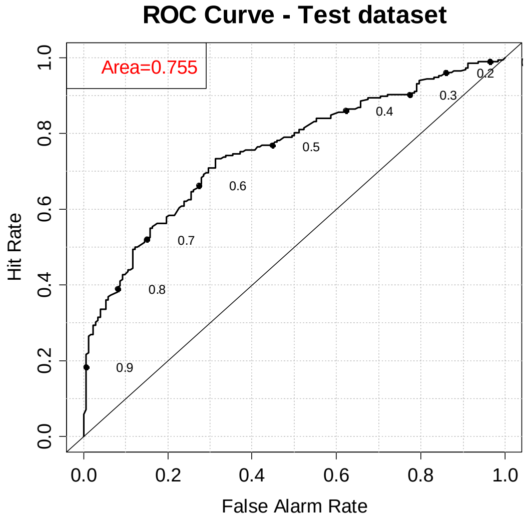
1000
1500
0
10
20
30
40
50
5
10
15
20
25
30
35

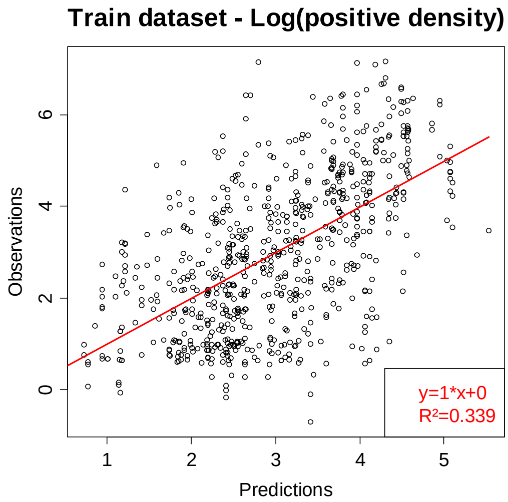

Trisopterus luscus
Raw data
Selectivity correction
Mean depth at length
Maximum length
Counts
0
1000
2000
3000
4000
5000
Depth (m)
0
10
20
30
40
50
5
10
15
20
25
30
35
Length (cm)

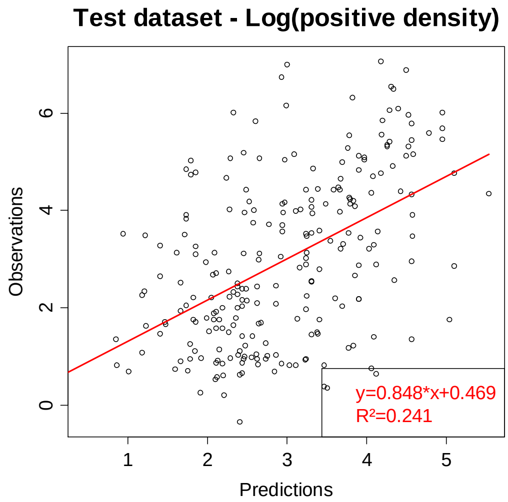
Appendix II: Validation results

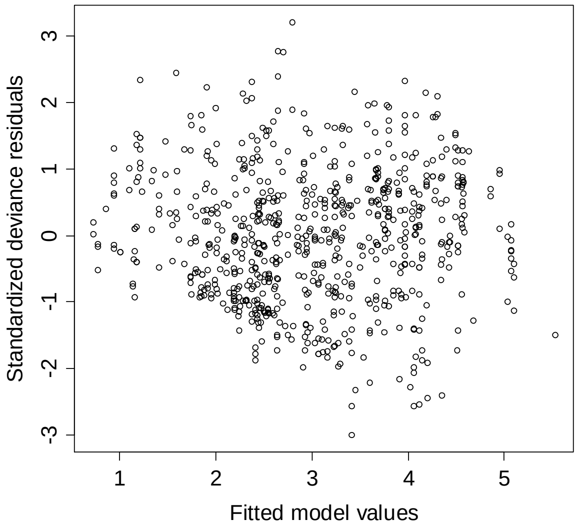
Solea solea



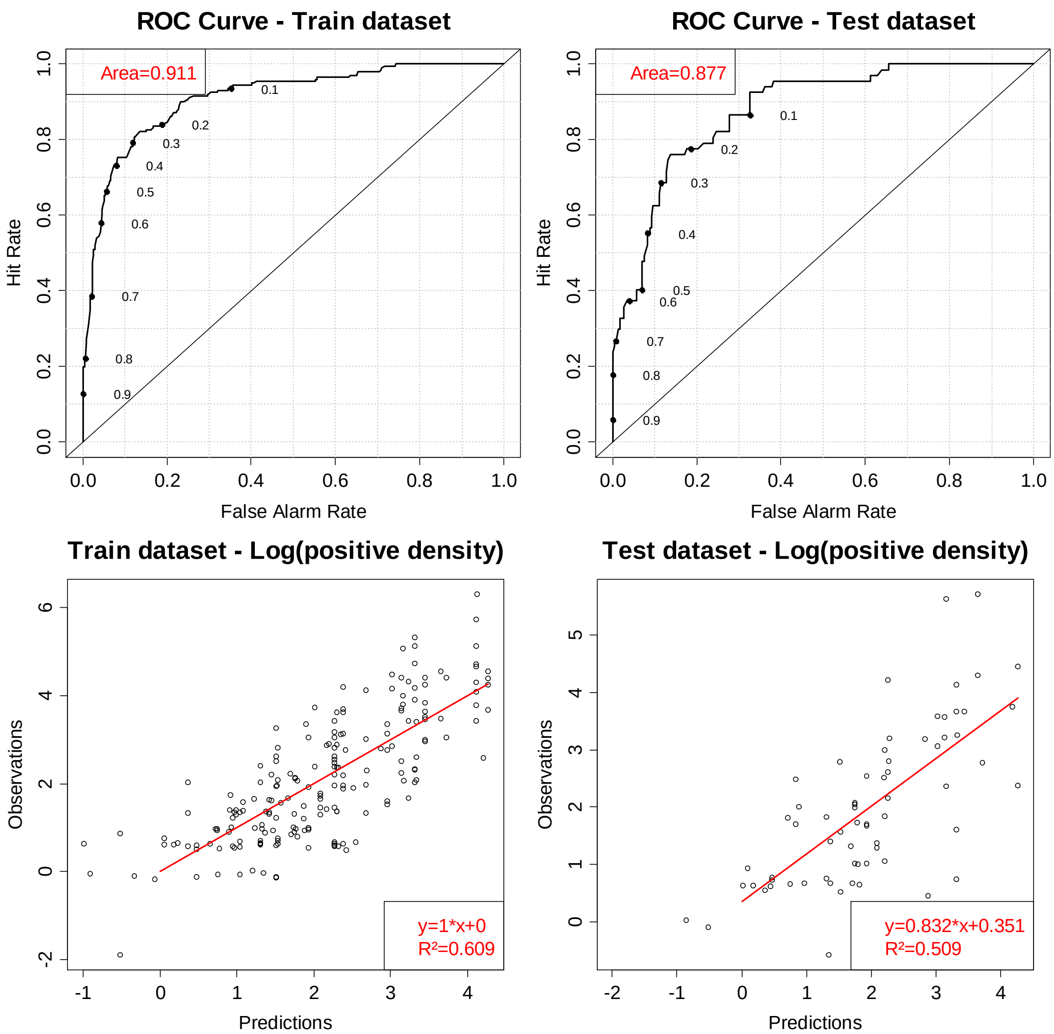


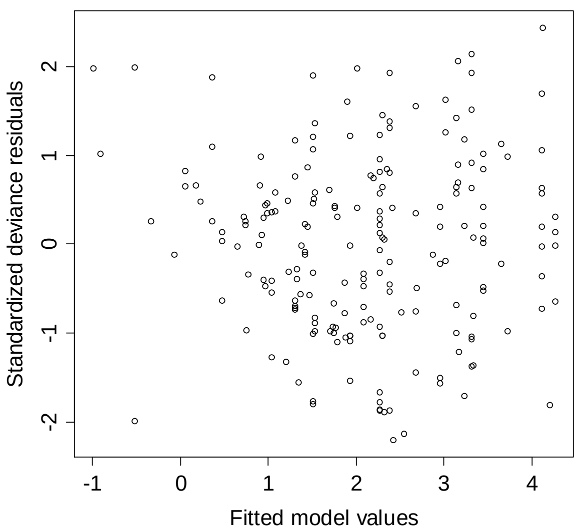




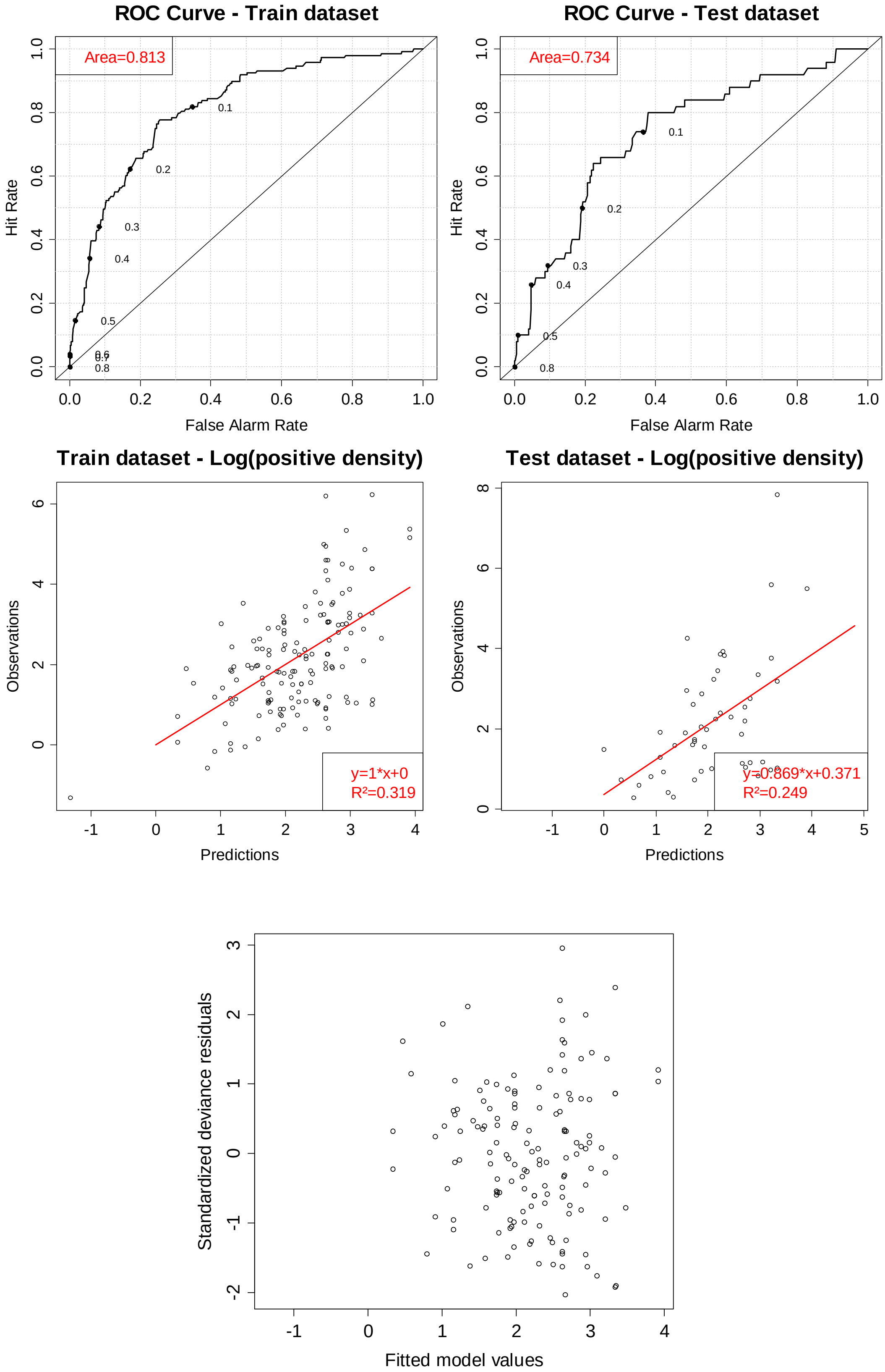


Pleuronectes platessa





Dicologlossa cuneata



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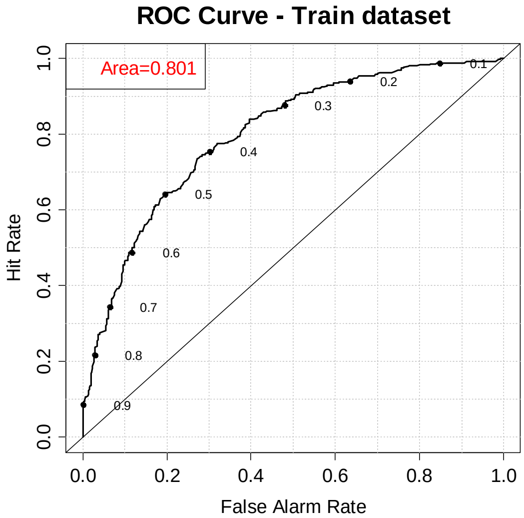
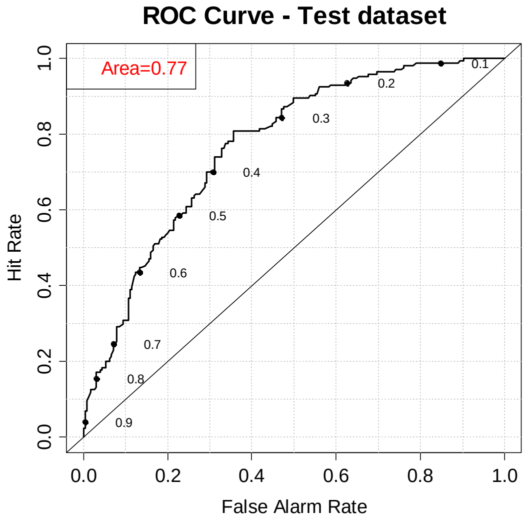
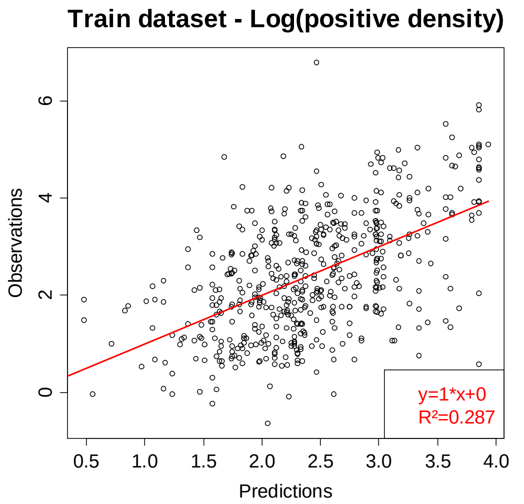
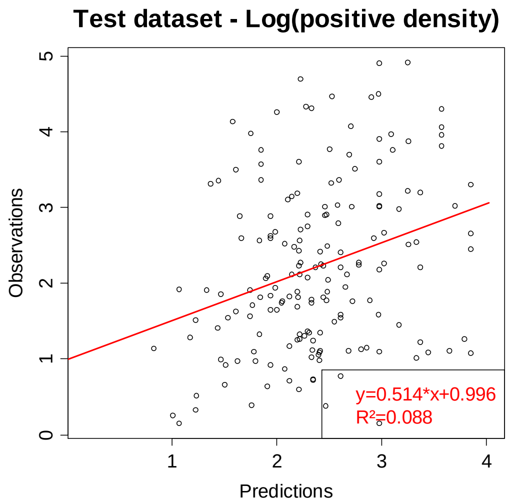
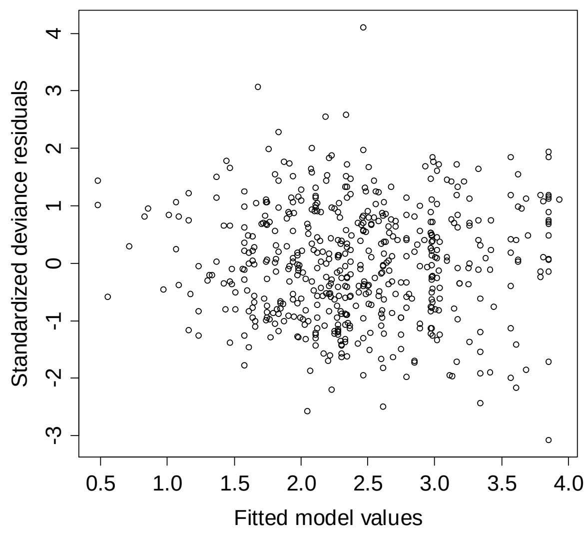


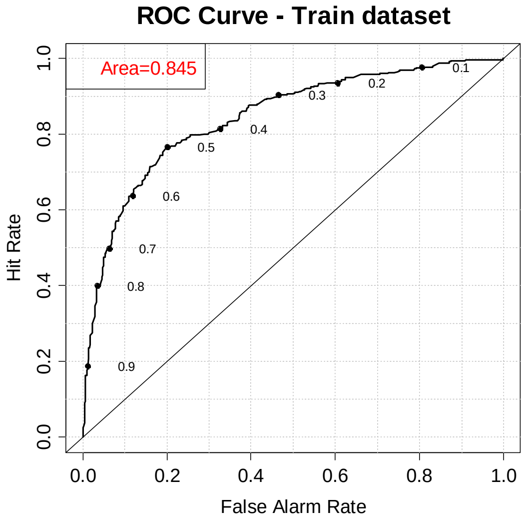


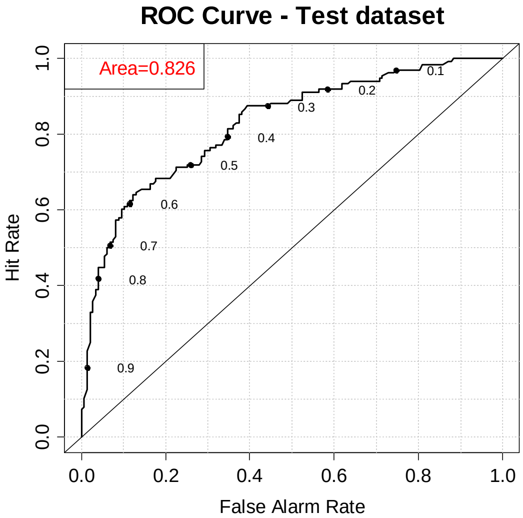


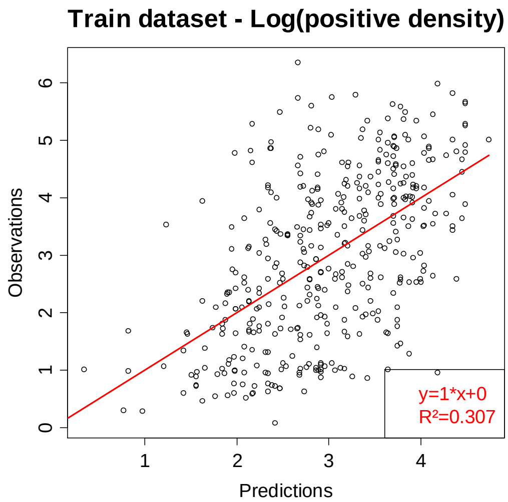


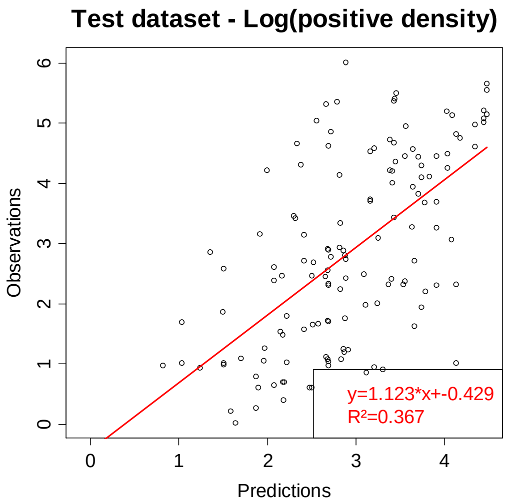


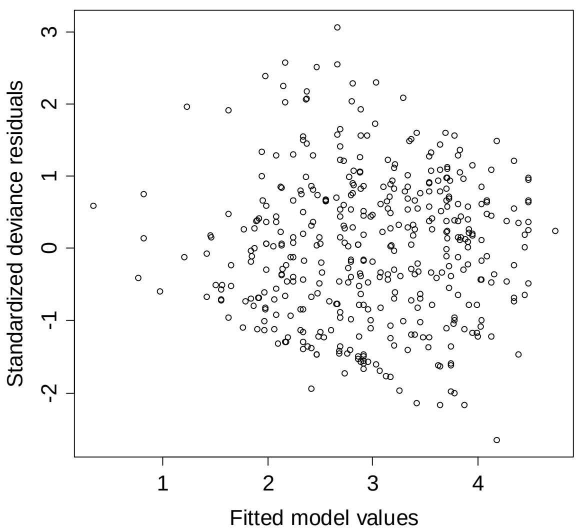
Merlangius merlangus



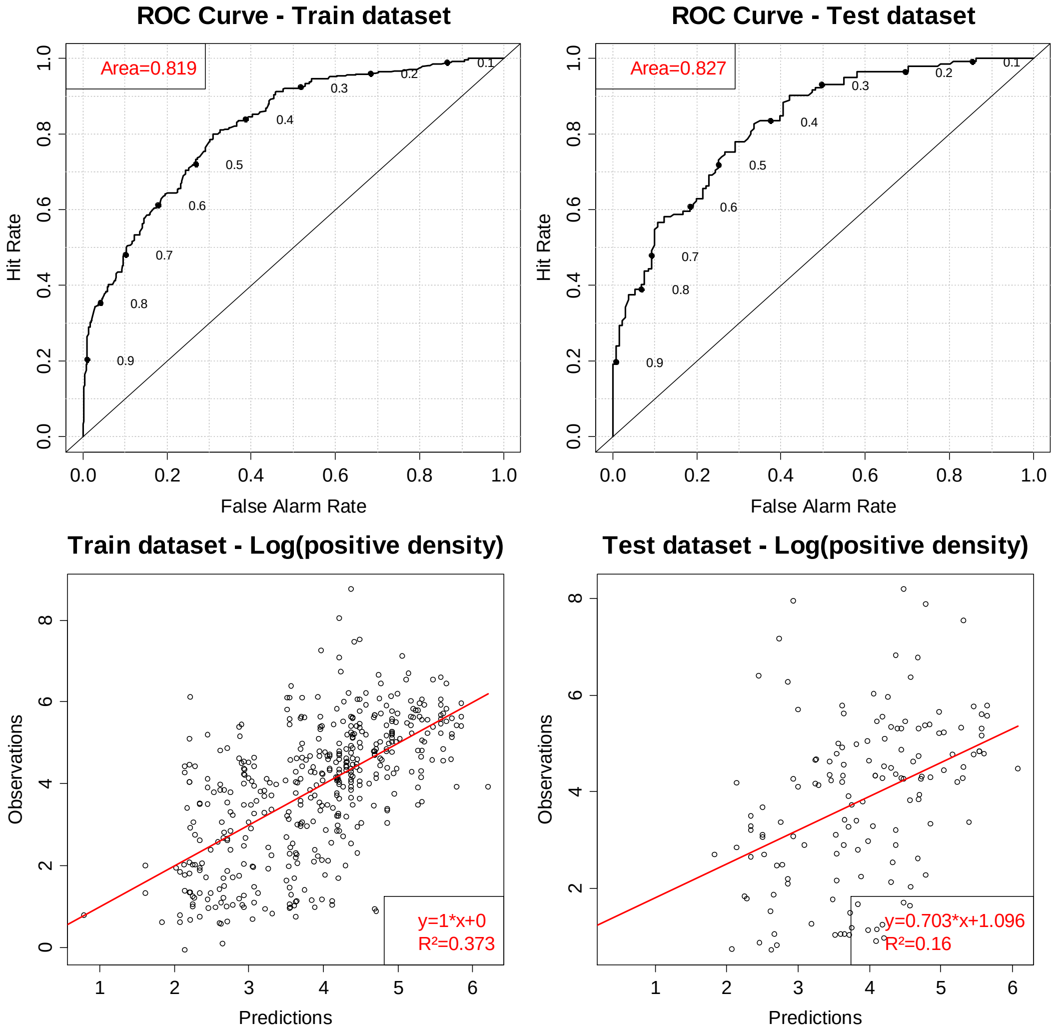


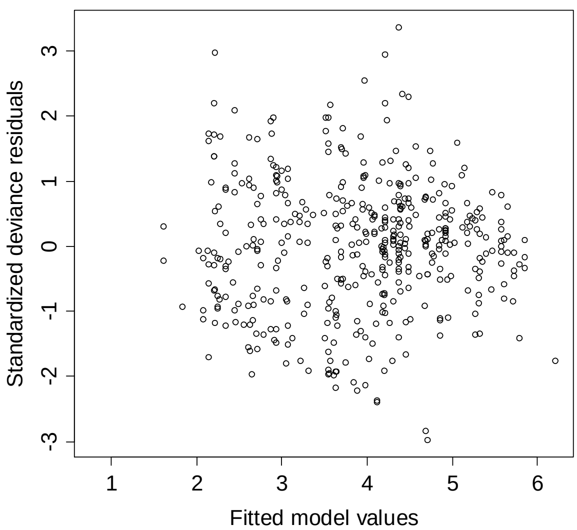






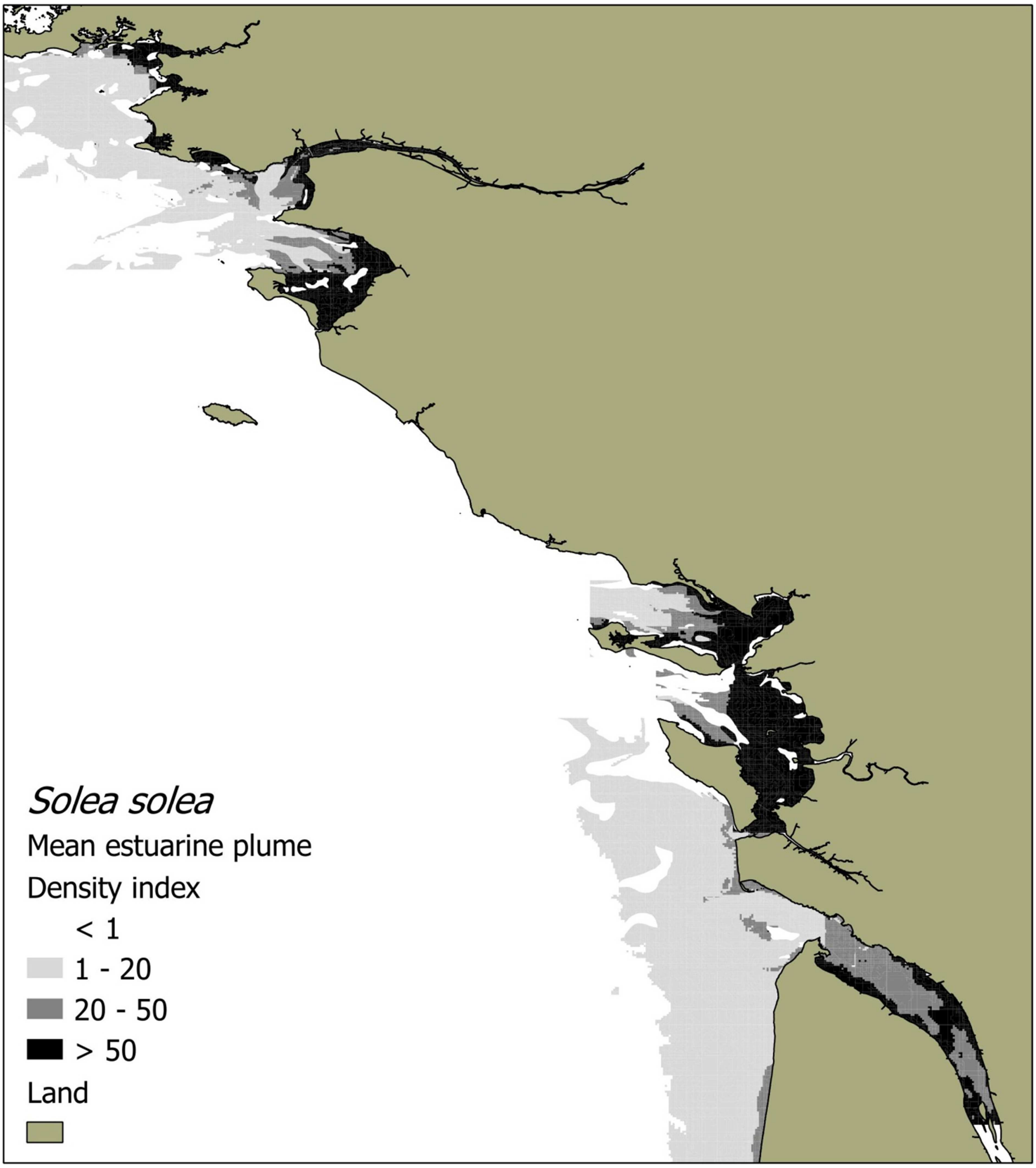
Trisopterus luscus

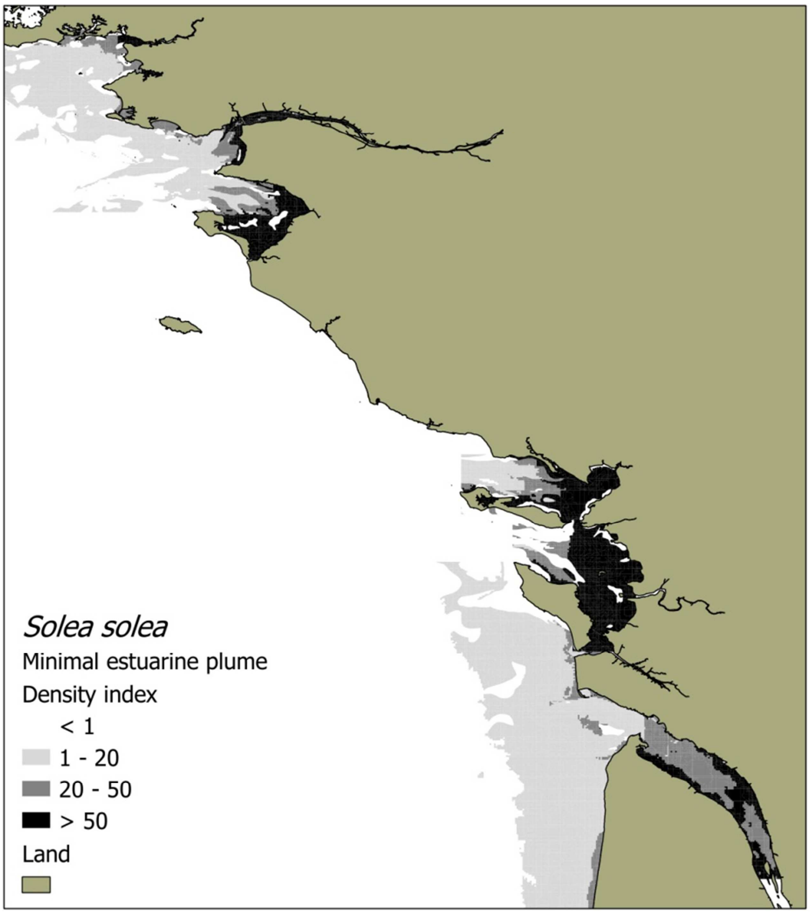


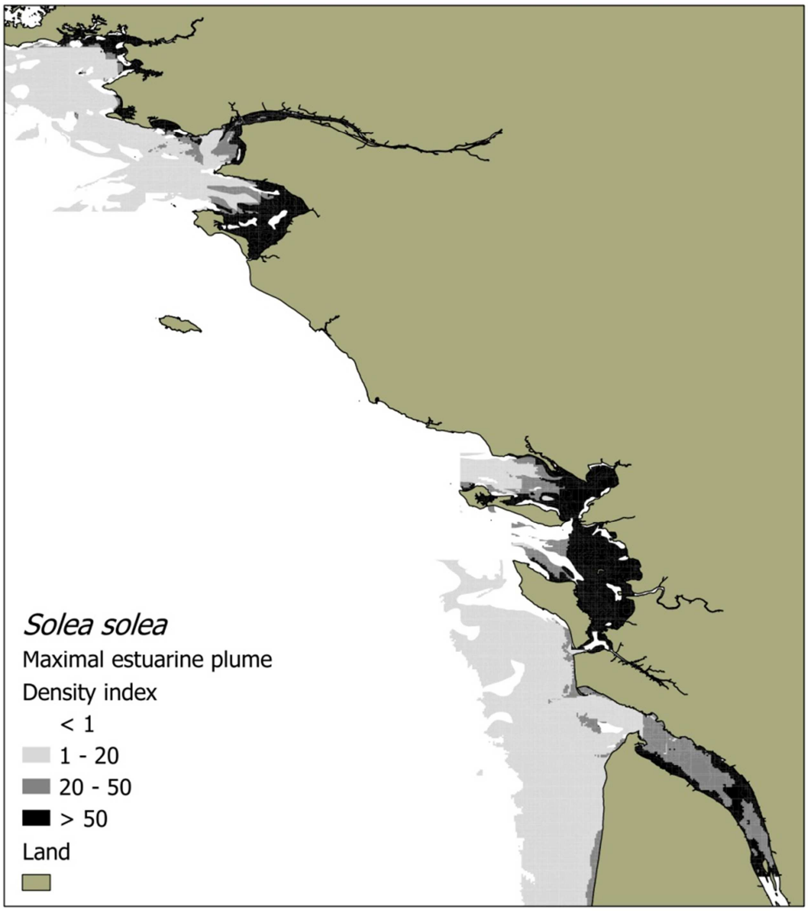


Appendix III: Density maps

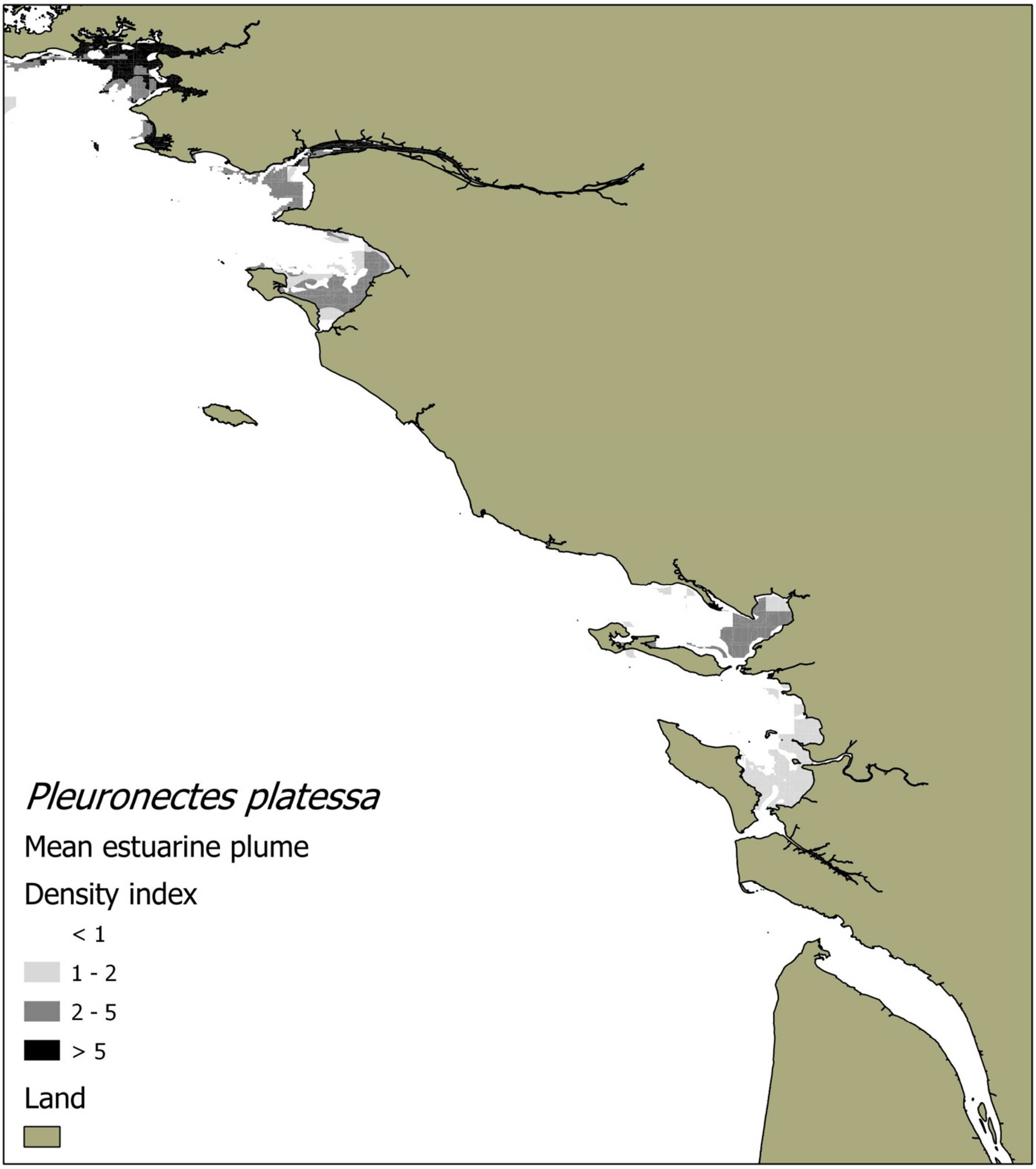
Solea solea

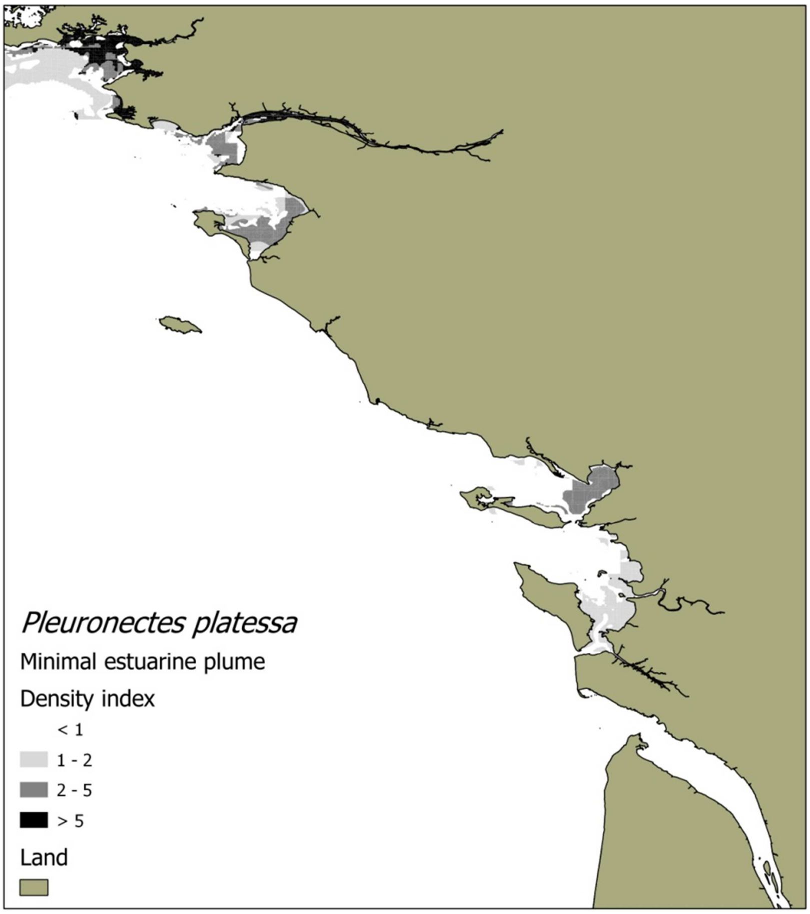


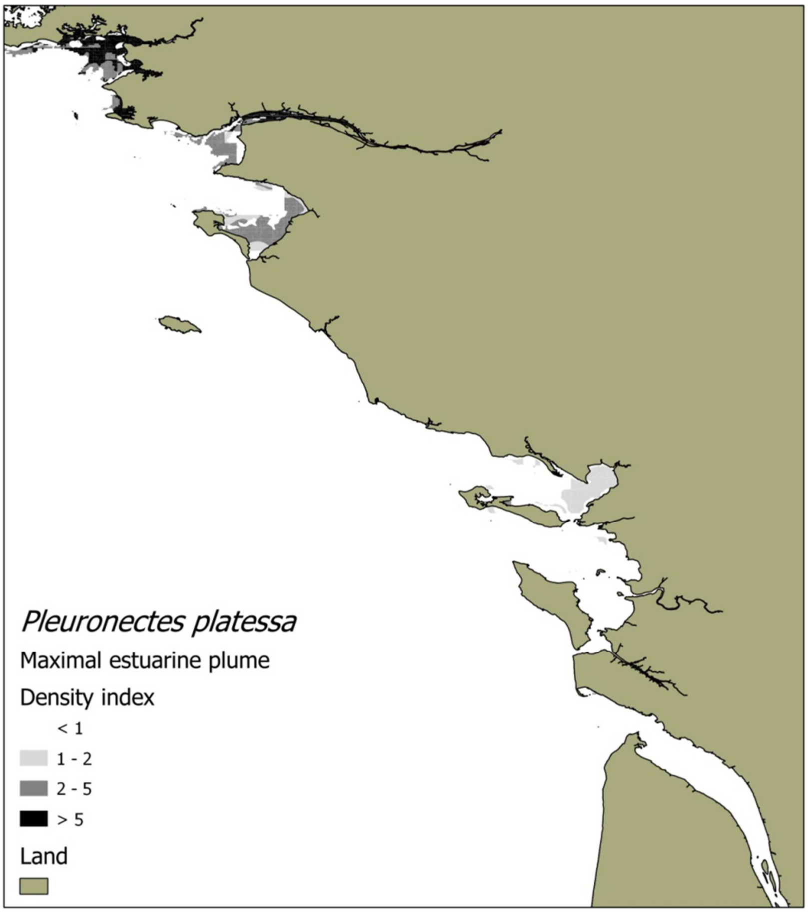

Solea solea
Minimal estuarine plume
Density index
< 1
1 - 20
20 - 50
> 50
Land


Solea solea
Maximal estuarine plume
Density index
< 1
1 - 20
20 - 50
> 50
Land

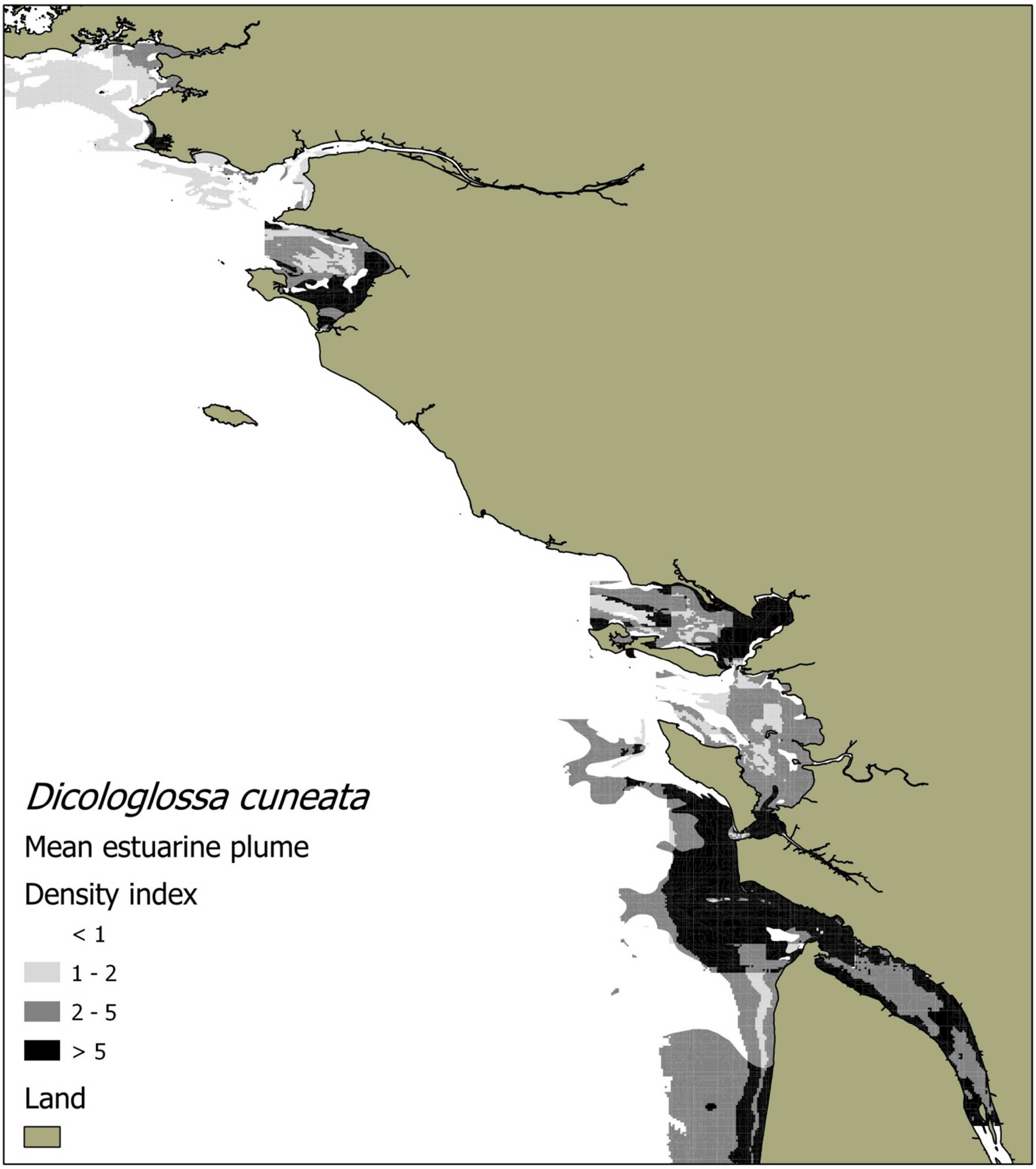
Pleuronectes platessa

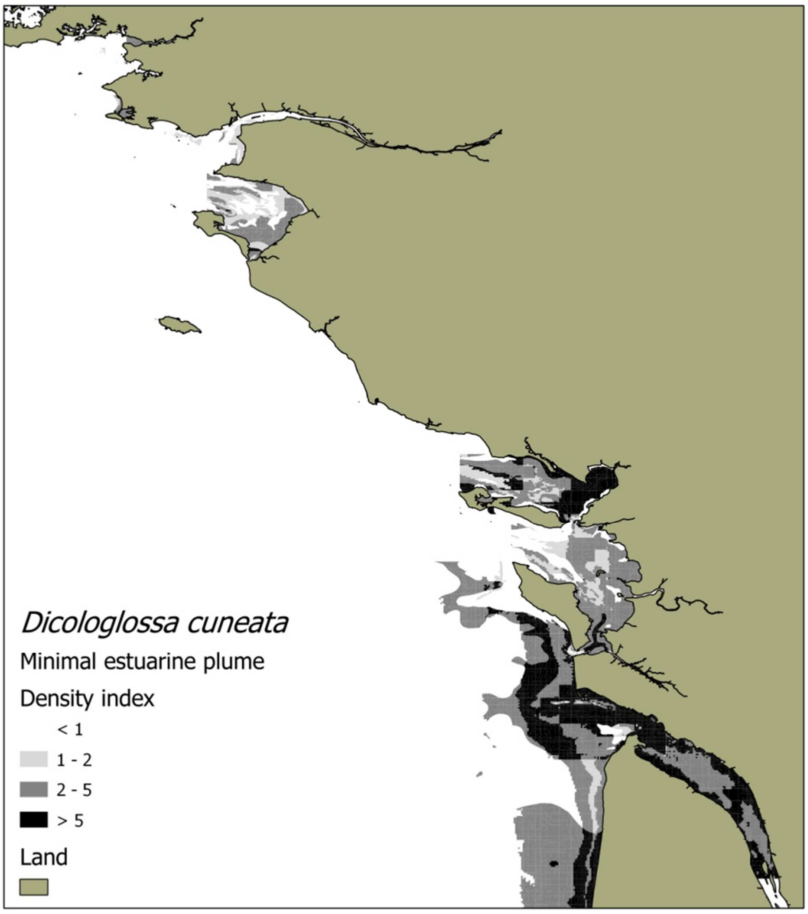



Pleuronectes platessa
Minimal estuarine plume
Density index
< 1
1 - 2
2 - 5
> 5
Land

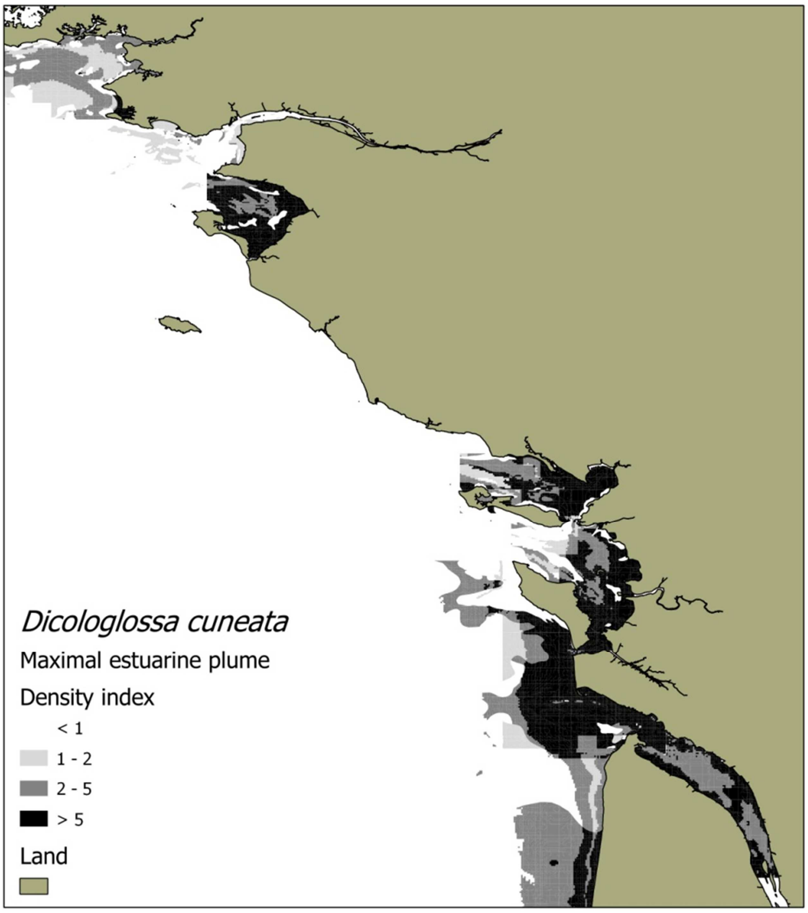

Pleuronectes platessa
Maximal estuarine plume
Density index
< 1
1 - 2
2 - 5
> 5
Land

Dicologlossa cuneata





Dicologlossa cuneata
Minimal estuarine plume
Density index
< 1
1 - 2
2 - 5
> 5
Land



Dicologlossa cuneata
Maximal estuarine plume
Density index
< 1
1 - 2
2 - 5
> 5
Land

Appendix IV: Contributions

Table 10: Relative contribution and area by class of factor under ***mean estuarine plume*** conditions

	Conditions	Solea s.		Pleuronectes p.		Dicologlossa c.	
Factor	Class	Contr. (%)	Area (%)	Contr. (%)	Area (%)	Contr. (%)	Area (%)
Salinity	> 32	56.3	50.7	14.7	41.0	31.5	50.7
	] 30 ; 32]	24.1	28.7	38.4	39.4	34.9	28.7
	< 30	19.7	20.5	46.9	19.6	33.6	20.5
Sediment	Mud	75.5	48.2	77.7	55.6	38.7	48.2
	Fine sand	18.7	32.4	10.0	13.4	55.6	32.4
	Coarse sand	5.8	19.4	12.3	31.0	5.7	19.4
Bathymetry	> -5	77.7	23.0	80.9	35.1	37.8	23.0
	] -10 ; -5]	11.4	17.9	13.0	17.1	16.6	17.9
	] -20 ; -10]	8.1	23.3	5.7	25.5	35.2	23.3
	] -36 ; -20]	2.8	35.9	0.5	22.3	10.4	35.9
Wave height	< 0.3	67.6	18.6	44.3	22.0	31.4	18.6
	] 0.3 ; 0.5]	15.2	8.2	20.2	16.6	6.7	8.2
	> 0.5	17.2	73.1	35.4	61.3	61.9	73.1
Geographic sector	Vilaine	4.6	10.3	55.3	21.6	4.1	10.3
	Loire	6.4	15.3	16.8	32.0	1.8	15.3
	Bourgneuf	13.1	5.9	12.6	12.2	6.5	5.9
	Pertuis Breton	14.9	7.4	8.5	15.4	9.5	7.4
	Pertuis Antioche	44.2	8.9	6.8	18.7	9.4	8.9
	Gironde	16.8	52.2			68.6	52.2

Relative contribution and area by class of factor under ***minimal estuarine plume*** conditions

	Conditions	Solea s.		Pleuronectes p.		Dicologlossa c.	
Factor	Class	Contr. (%)	Area (%)	Contr. (%)	Area (%)	Contr. (%)	Area (%)
Salinity	> 32	82.9	81.0	75.8	85.6	61.6	81.0
	] 30 ; 32]	2.6	7.2	11.1	8.6	10.3	7.2
	< 30	14.5	11.8	13.1	5.8	28.0	11.8
Sediment	Mud	76.2	48.2	77.9	55.6	43.0	48.2
	Fine sand	18.1	32.4	9.8	13.4	51.6	32.4
	Coarse sand	5.6	19.4	12.3	31.0	5.4	19.4
Bathymetry	> -5	78.3	23.0	79.5	35.1	39.6	23.0
	] -10 ; -5]	11.2	17.9	14.1	17.1	16.0	17.9
	] -20 ; -10]	7.7	23.3	5.9	25.5	32.1	23.3
	] -36 ; -20]	2.8	35.9	0.5	22.3	12.3	35.9
Wave height	< 0.3	68.9	18.6	44.1	22.0	36.4	18.6
	] 0.3 ; 0.5]	14.9	8.2	20.2	16.6	7.2	8.2
	> 0.5	16.2	73.1	35.7	61.3	56.4	73.1
Geographic sector	Vilaine	3.6	10.3	56.8	21.6	2.2	10.3
	Loire	5.9	15.3	16.3	32.0	1.5	15.3
	Bourgneuf	13.0	5.9	12.6	12.2	4.0	5.9
	Pertuis Breton	15.3	7.4	8.0	15.4	11.8	7.4
	Pertuis Antioche	45.5	8.9	6.4	18.7	11.0	8.9
	Gironde	16.7	52.2			69.3	52.2

Relative contribution and area by class of factor under ***maximal estuarine plume*** conditions

	Conditions	*Solea s.*		*Pleuronectes p.*		*Dicologlossa c.*	
Factor	Class	Contr. (%)	Area (%)	Contr. (%)	Area (%)	Contr. (%)	Area (%)
Salinity	> 32	7.5	33.2	1.9	11.1	14.0	33.2
	] 30 ; 32]	45.6	25.0	12.9	29.2	34.8	25.0
	< 30	46.9	41.9	85.3	59.7	51.2	41.9
Sediment	Mud	74.7	48.2	78.6	55.6	43.4	48.2
	Fine sand	18.8	32.4	9.8	13.4	50.3	32.4
	Coarse sand	6.5	19.4	11.6	31.0	6.3	19.4
Bathymetry	> -5	77.9	23.0	82.2	35.1	43.4	23.0
	] -10 ; -5]	11.1	17.9	12.7	17.1	16.1	17.9
	] -20 ; -10]	8.2	23.3	4.7	25.5	31.6	23.3
	] -36 ; -20]	2.8	35.9	0.4	22.3	8.8	35.9
Wave height	< 0.3	67.8	18.6	44.7	22.0	35.1	18.6
	] 0.3 ; 0.5]	14.8	8.2	21.0	16.6	8.2	8.2
	> 0.5	17.5	73.1	34.3	61.3	56.6	73.1
Geographic sector	Vilaine	5.1	10.3	55.8	21.6	5.2	10.3
	Loire	6.0	15.3	18.5	32.0	1.5	15.3
	Bourgneuf	17.0	5.9	10.6	12.2	9.7	5.9
	Pertuis Breton	14.2	7.4	8.6	15.4	12.3	7.4
	Pertuis Antioche	42.3	8.9	6.5	18.7	13.8	8.9
	Gironde	15.4	52.2			57.5	52.2

Diplôme : Ingénieur de l'Institut Supérieur des Sciences Agronomiques, Agroalimentaires, Horticoles et du Paysage

Spécialité : Halieutique
Spécialisation / option : Ressources et Écosystèmes Aquatiques
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Titre français : Description quantitative de l'habitat pour les juvéniles de sept espèces de poissons dépendantes des zones côtières et estuariennes dans le Golfe de Gascogne
Titre anglais : Quantitative description of habitat for the juveniles of seven estuarine and coastal dependent fish species in the Bay of Biscay

Résumé : Estuaires et zones côtières sont importants pour de nombreuses espèces de poissons de par leur fonction de nourriceries et donc d'habitats essentiels. La diminution et la dégradation de l'habitat sont des phénomènes répandus dans ces zones qui doivent donc être protégées pour le renouvellement des populations. Modèles linéaires généralisés et systèmes d'information géographiques ont été combinés pour identifier les habitats essentiels en utilisant des paramètres physiques connus pour influencer la répartition spatiale et la densité des juvéniles : bathymétrie, sédiment, influence estuarienne. La hauteur de vague a aussi été testée comme proxy de l'exposition de la côte, qui a été évoquée comme une variable explicative potentielle de la qualité de l'habitat des juvéniles de poissons plats. Des cartes de densité ont été produites et les contributions relatives des différents types d'habitats à la population totale de juvéniles ont été calculées. Seuls les juvéniles de poissons plats on été cartographiés. Les zones peu profondes et vaseuses abritent 60% de la population totale des juvéniles de *Solea solea* et *Pleuronectes platessa* alors qu'elles ne représentent que 16% de la zone étudiée. Elles peuvent donc être considérées comme des habitats essentiels pour ces deux espèces. La hauteur de vague a été significative pour ces deux espèces et explique leur préférence pour des zones abritées, i.e. les baies semi-encloses. Les cartes de répartition des juvéniles de *Pleuronectes platessa* et *Dicologlossa cuneata* a révélé des tendances spatiales et temporelles qui ont été expliquées par les limites de répartitions de ces deux espèces et des tendances environnementales.

Abstract: Estuaries and coastal areas are important for many fish species due to their habitat function as nursery spots which make them essential habitats. Habitat reduction and degradation are common phenomena on these areas and protection of such sites is therefore essential for recovery of fish population. Generalized Linear Models (GLM) and Geographic Information System (GIS) software were combined to provide identification of fish essential habitats for seven fish species using physical parameters known to influence fish spatial repartition and density: bathymetry, sediment, estuarine influence. Wave height has also been tested as a proxy for coastal exposure which has been evocated as a plausible explanatory variable of juvenile flatfish habitat suitability. Density maps have been produced and relative contributions of the different abitats to the total juveniles' population have been computed. Only flatfish were retained for mapping process. Shallow and muddy areas contributed to 60% of total juveniles' population of *Solea solea* and *Pleuronectes platessa* whereas only representing 16% of the study area and can therefore be considered as essential habitats for these two species. Wave height was significant for both species and explains their predilection for sheltered areas, i.e. semi-enclosed bays. Repartition maps of juveniles from *Pleuronectes platessa* and *Dicologlossa cuneata* revealed spatial and temporal trends which were explained thanks to the limits of repartition for these two species and environmental trends.

Mots-clés : Espèces dépendantes des zones côtières et estuariennes ; Nourriceries ; Modèles d'habitat ; Système d'Information Géographique ; Golfe de Gascogne
Key Words: Coastal and nursery dependent species; Nursery ground; Habitat suitability models; Geographic Information System; Bay of Biscay