
A quantitative estimate of the function of soft-bottom sheltered coastal areas as essential flatfish nursery habitat

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Abstract:

Essential fish habitat suitability (EFHS) models and geographic information system (GIS) were combined to describe nursery habitats for three flatfish species (*Solea solea*, *Pleuronectes platessa*, *Dicologlossa cuneata*) in the Bay of Biscay (Western Europe), using physical parameters known or suspected to influence juvenile flatfish spatial distribution and density (*i.e.* bathymetry, sediment, estuarine influence and wave exposure). The effects of habitat features on juvenile distribution were first calculated from EFHS models, used to identify the habitats in which juveniles are concentrated. The EFHS model for *S. solea* confirmed previous findings regarding its preference for shallow soft bottom areas and provided new insights relating to the significant effect of wave exposure on nursery habitat suitability. The two other models extended these conclusions with some discrepancies among species related to their respective niches. Using a GIS, quantitative density maps were produced from EFHS models predictions. The respective areas of the different habitats were determined and their relative contributions (density × area) to the total amount of juveniles were calculated at the scale of stock management, in the Bay of Biscay. Shallow and muddy areas contributed to 70% of total juvenile relative abundance whereas only representing 16% of the coastal area, suggesting that they should be considered as essential habitats for these three flatfish species. For *S. solea* and *P. platessa*, wave exposure explained the propensity for sheltered areas, where concentration of juveniles was higher. Distribution maps of *P. platessa* and *D. cuneata* juveniles also revealed opposite spatial and temporal trends which were explained by the respective biogeographical distributions of these two species, close to their southern and northern limit respectively, and by their responses to hydroclimatic trends.

Keywords: coastal and estuarine dependent species ; nursery ground ; habitat suitability models ; Geographic Information System ; Bay of Biscay

1. Introduction

Coastal and estuarine nursery habitats are essential for many marine fish species (Peterson et al., 2000, Beck et al., 2001 and Fulford et al., 2011), particularly for flatfish (Miller et al., 1984 and Able, 2005). The suitability of these habitats influences juvenile growth and survival rates (Rijnsdorp et al., 1992 and Gibson, 1994) and can act as habitat bottlenecks (Iles and Beverton, 2000). As a consequence, the vulnerability of coastal habitats to anthropogenic stressors (França et al., 2012, Halpern et al., 2007 and Halpern et al., 2008) can alter recruitment and future population renewal. Relationships between species and their habitats are a central issue to characterize the mechanisms determining habitat suitability. However, there is a lack of quantitative evidence of the importance of habitat suitability in patterns driving population dynamics. Despite the high number of studies which have focused on coastal habitat use by fish species, the value of habitats for fish population dynamics seldom remains quantified (Levin and Stunz, 2005 and Fodrie et al., 2009). One required approach to bridge this gap from knowledge to quantitative estimates of EFHS consists of predicting geographic distributions of populations at different life stages, and especially for juveniles on nursery grounds, through habitat mapping (Rubec et al., 1999 and Lauria et al., 2011). EFHS maps could constitute essential elements for prioritizing areas for conducting spatial ecosystem assessments (Brown et al., 2000 and Cogan et al., 2009). They may solve questions about what constitutes high-value fish habitat for exploited species (Fodrie and Mendoza, 2006) and provide information needed for conservation purpose

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(Stoner, 2003). The identification and mapping of essential fish habitats, especially nursery grounds, may also help to prioritize management measures. Especially, such maps would be appropriate for Marine Protected Areas design, to insure that they are efficient in maintaining the potential of marine living resources renewal.

The Bay of Biscay, an arm of the North Atlantic indenting the west coast of France (ICES Division Area VIIIa/b; Fig. 1), is considered to be a stock management unit for many exploited marine fish species (Anon., 2011). The inshore waters of the Bay of Biscay support nursery areas for several commercially important species, notably flatfishes (Hermant *et al.*, 2010). Estuaries and coastal areas have been studied for several decades in the Bay of Biscay and a large amount of scientific data on fish abundance is available (Brind'Amour and Lobry, 2009). For *S. solea*, Le Pape *et al.* (2003b) provided maps of density index over the Bay of Biscay and identified essential habitats. To follow up this first approach, the present studies aimed at achieving two objectives:

- The previous quantitative description of habitat suitability for the *S. solea* population of the Bay of Biscay was conducted to develop an early quantitative assessment of its nursery habitats using bathymetry, sediment structure and estuarine influence. EFHS model has been used to identify the habitats in which juvenile *S. solea* were concentrated. Similar approaches on juvenile *S. solea* were previously developed in the Eastern Channel (Riou *et al.*, 2001; Eastwood *et al.*, 2003; Rochette *et al.*, 2010) and along the Portuguese coasts (Vasconcelos *et al.*, 2010) with the same conclusions about the interest of shallow soft bottom areas inside or near estuarine influence. However, all these EFHS model based on the distribution of young of the year (0-group) *S. solea* led to a high non explained variability (*e.g.*, in the Bay of Biscay: > 70% for model including both descriptors of habitat features and mesoscale variability among geographical sectors but close to 90% when only habitat descriptors were used; Le Pape *et al.*, 2003b). The first objective of the present study was to improve the EFHS model for juvenile *S. solea*. Several studies have shown that coastal exposure affects habitat structure and juveniles of most flatfish species prefer sheltered parts of the coast and embayments (Howell *et al.*, 1999). However, few studies have quantified the impact of coastal exposure (Pihl and van der Veer, 1992) and integrated its effect in EFHS mapping (Maxwell *et al.*, 2009; for adult fish including *S.*

1
2 *solea*). Indicators for wave exposure of the coastal areas were thus used to improve the description of
3 nursery habitat suitability (Fodrie and Mendoza, 2006) in the Bay of Biscay.

4 - *S. solea* was the single studied species in previous juvenile fish habitat mapping approaches
5 in the Bay of Biscay. Thus there is a need to assess the impact of the habitat descriptors and potentially
6 extend the mapping procedure to other estuarine and coastal dependent flatfish species. The two other
7 most common estuarine and coastal dependent flatfish species during the last three decades (*P.*
8 *platessa*, *D. cuneata*; Désaunay *et al.*, 2006; Hermant *et al.*, 2010) were selected in addition to *S.*
9 *solea*, both being of interest for fisheries. *P. platessa* has a life history similar to *S. solea*, characterized
10 by winter offshore spawning areas, post-larvae settling on inshore nursery grounds during spring and
11 juveniles growing within nursery areas until they mature to adult age and move to the continental shelf
12 (Koutsikopoulos *et al.*, 1991, Hermant *et al.*, 2010). The coastal nursery dependence of *D. cuneata* is
13 similar but this species is a summer spawner (Hermant *et al.*, 2010). The juvenile distribution patterns
14 of juvenile *P. platessa* has been investigated from habitat suitability models and/or quantitative
15 mapping procedure in numerous other areas in Western Europe, the Baltic (Pihl *et al.*, 2000;
16 Wennhage *et al.*, 2007), the North Sea (van der Veer *et al.*, 2011) and the Eastern Channel (Riou *et al.*,
17 2001). These studies described *P. platessa*'s preference for shallow soft bottom areas and pointed out
18 the interest to include coastal exposure as descriptor of habitat suitability. On the contrary, knowledge
19 on *D. cuneata* is scarce, without any existing quantitative estimate of habitat suitability.

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22 The analysis is based on 0-group of these three species on which data have been gathered from
23 surveys conducted over a 30-year period throughout the estuarine and coastal areas of the Bay of
24 Biscay. Achievement of the two objectives relies on quantitative mapping based on the relation
25 between 0-group flatfish densities and habitat descriptors to identify nursery habitats of major
26 importance. EFHS models were developed from generalized linear models to describe habitat related
27 patterns in flatfish juvenile distribution. Then, these models outputs and Geographic Information
28 System (GIS) were combined to provide quantitative habitat maps and relative contributions of the
29 different habitats to the total proportion of juvenile flatfish at the scale of the Bay of Biscay
30 population, while accounting for interannual variability.

2. Material and Methods

2.1. Fish survey data

The study area

The Bay of Biscay study area (Fig.1) includes six major nurseries (Le Pape *et al.*, 2003b) which have been considered as independent sectors due to the coastal morphology: Vilaine, Loire and Gironde, three estuaries, and Bourgneuf, Pertuis Breton and Pertuis d'Antioche, three bays. Other coastal sectors of the Bay of Biscay were considered as unsuitable nursery areas from previous approaches (Le Pape *et al.*, 2003b) and were not included in the analysis. As the 6 considered sectors constitute almost the entire area of repartition at the scale of the Bay of Biscay for the juveniles of the three considered species, extrapolation at the scale of the management unit (Bay of Biscay) can be performed. As this study focuses on marine species, the study area was restricted to the upstream limit of the oligohaline zone (*i.e.* higher than 5PSS, the limit of marine species extent; Courrat *et al.*, 2009; Nicolas *et al.*, 2010; Rochette *et al.*, 2010) within rivers. The off-shore limit was set at the 35m isobath, as juveniles of flatfish species are scarcely present in deeper waters (Riou *et al.*, 2001).

Scientific trawl surveys data in the coastal areas of the Bay of Biscay

Data from beam trawl surveys focusing on marine juveniles fish, conducted on soft bottoms throughout the coastal areas of Bay of Biscay from the 1980s up to present by three different scientific institutes have been gathered. The six aforementioned nurseries have been repeatedly sampled over this period (Table 1). Most of these surveys were conducted from late summer to mid-autumn; a period considered as appropriate to study flatfish nursery grounds (*i.e.* relatively stable density and distribution pattern of juvenile flatfish which are representative of the nursery function during the productive period; Dorel *et al.*, 1991; Courrat *et al.*, 2009). Only trawl hauls performed between the end of August and mid-October were selected for the study; they originated from three different sources (Table 1):

- IFREMER (France). Data used in this study originated from the same surveys series as the ones used by Le Pape *et al.* (2003b). These series were upgraded with the surveys conducted from 2000 to 2010 (Brind'Amour and Lobry, 2009; Hermant *et al.*; 2010 and further) in the six studied nursery sectors with the same sampling protocol (+35% of trawl hauls from recent IFREMER survey series compared to Le Pape *et al.*, 2003b),
- IRSTEA (France). French estuaries were investigated (Courrat *et al.*, 2009) in the context of the European Water Framework Directive (WFD). These new surveys provided additional data in the inner part of the Gironde, Loire and Vilaine estuaries (Courrat *et al.*, 2009; Delpech *et al.*, 2010),
- BIO-LITTORAL (France), a scientific consultancy operated an additional survey in 2008 in the Loire estuary, following the same procedure than IRSTEA.

In all of these surveys, the gear used was a 3-m wide beam trawl with a 20-mm stretched mesh in the cod end. Hauls were made only in daylight and performed at an average speed of 2.5 knots, ranging from 1.5 to 3 knots, for 10 to 20 min. Further details about the sampling protocol can be found in Brind'Amour and Lobry (2009) and Delpech *et al.* (2010). 1643 trawl hauls (Table 1) showing no sign of tearing nor clogging were retained.

All flatfish caught were identified at the species level, counted and measured. As the aim of this study was to assess nursery habitats, the catches of 0-group were selected. This selection was done using a maximal length at age 0 for each species (15, 18 and 11 cm for *S. solea*, *P. platessa* and *D. cuneata* respectively; Hermant *et al.*, 2010).

Correcting the data: use of a selectivity factor

The density indices, in number of fish from 0-group, were first calculated for each 1-cm size class on each trawl haul from the selected data. As smaller fishes are subject to gear escapement, a correction function, depending on both gear and species parameters was used to reevaluate the catch for each size class of each species. The recalculated amount of juveniles at length L for the species s , in the trawl haul t , $N_{est,s,t}(L)$, is given in Eq.(1):

$$N_{est,s,t}(L) = \frac{N_{caught,s,t}(L)}{S_s(L)} \quad (1)$$

where $N_{\text{caught},s,t}(L)$ is the amount of catch of juveniles of length L for the species s in the trawl haul t , and $S_s(L)$ is the corrected proportion of juveniles of length L and species s selected by a beam trawl with a 20mm mesh size (i.e. coefficient of selectivity). The calculation (Eq.(2)) of $S_s(L)$ is based on Dardignac and de Verdelhan (1978) adapted from Rochette *et al.* (2010):

$$S_s(L) = \frac{\exp\left[\left(\frac{2 \times L_S 50_M \times \log 3}{\Delta_{M,s}}\right) \times \left(\frac{L}{L_S 50_M} - 1\right)\right]}{1 + \exp\left[\left(\frac{2 \times L_S 50_M \times \log 3}{\Delta_{M,s}}\right) \times \left(\frac{L}{L_S 50_M} - 1\right)\right]} \quad (2)$$

where L is the length, in mm, $L_S 50_M = \alpha_S \cdot M$ the 50% retention length, where M is the stretched mesh size in mm (here 20), and $\Delta_{M,s} = \beta \cdot L_S 50_M$ the selectivity range, *i.e.* the difference between 75% and 25% retentions lengths. According to the similar shape of the two species, the α_S parameter of *S. solea* (3.3; Rochette *et al.*, 2010) has been used for *D. cuneata*, another value being used for *P. platessa* (2.3; Anon., 1998). β parameter is considered common for all species (0.385, Rochette *et al.*, 2010).

0-group density indices were calculated for the three species on each trawl haul accounting for the size structure of the catches by summing the recalculated catch divided by the sampled surface (Eq.(3)):

$$\text{Density indice}_{s,t} = \frac{\sum_L N_{Est,s,t}(L)}{\text{Surface}_t} \quad (3)$$

As the catchability of these species by the beam trawl is unknown, density indices of 0-group juveniles for the three studied flatfish provided only relative information, sufficient to estimate standardized habitat related patterns but not to calculate the real overall abundance of juvenile fish present in the trawled area.

2.2. Information on physical descriptors

Data on physical parameters known or suspected to influence the repartition of coastal and estuarine nursery dependent species at the local stage, *i.e.* bathymetry, sediment, estuarine plume and wave exposure, were collected over the study area (Table 1):

Bathymetry

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2 A raster map of bathymetry was available as continuous numerical values. Bathymetry data
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4 have been cut into 4 classes:] -36m ; -20m],] -20m ; -10m],] -10m ; -5m] and > -5m up to the
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6 coastline.

Sediment structure

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10 A sediment structure map was created as a combination of two sources. A sediment map of the
11
12 Bay of Biscay was the main source of information. Five classes of sediments were available: mud, fine
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14 sand, coarse sand, gravels, and rocks. Gravel and coarse sand have been pooled and rocky areas were
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16 excluded, as they do not host the considered flatfish species. Additional information on sediment from
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18 the inner Loire estuary was merged to this map to cover the trawl survey area.

Salinity

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22 Salinity is included in habitat suitability models to describe the positive influence of winter-
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24 spring estuarine plumes and their interannual variations on flatfish habitat (Le Pape et al., 2003ab;
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26 Kostecki *et al.*, 2010) and not to describe the hydrology and its short term influence on juvenile
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28 flatfish distribution, low at the end of the summer after a low river flow period in the Bay of Biscay
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30 (Le Pape et al., 2003a).

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34 A 3D hydrodynamic model (ECOMARS 3D; Lazure, 2009) was set up over the Bay of
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36 Biscay, providing standardized surface salinity from 1972 to 2011 every 6 hours (Huret *et al.*, 2013).
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38 Salinity data were extracted from the surface layer and averaged over the first four months of each
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40 year (January to April) on each cell of the spatial grid. Surface salinity from January to April is used as
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42 an inverse spatialized proxy of estuarine influence which depends on the river flows (the less the
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44 surface salinity, the more the river flows). This period has been chosen from previous analysis on *S.*
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46 *solea*, as it is most likely the time at which river discharge reaches its maximum (Le Pape et al.,
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48 2003d) and determines trophic chain enrichment (Kostecki *et al.*, 2010), thus nursery habitat and
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50 flatfish juveniles spatial distribution during the following critical spring-summer growth period (Le
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52 Pape *et al.*, 2003a). In the model, salinity is split into three classes: < 30,] 30 ; 32] and > 32, which
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54 correspond to estuarine waters, mixing zone and marine waters respectively. One annual raster map of
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56 average January –April surface salinity was finally available for each year of survey.
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Coastal exposure

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2 Data from the pre-operational system PREVIMER (<http://www.previmer.org/en/produits>)
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4 provided wave height (in m) every 3 hours, from 2002 to 2011 on a 2km horizontal regular grid
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6 covering the whole study area. The period selected for averaging wave height (May to August) was
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8 chosen for its overlap with the spring-summer growth period of juvenile flatfish on their nursery
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10 grounds (Dorel et al., 1991) before the surveys. This average wave height represents the level of wave
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12 exposure of coastal and estuarine habitats during the period when 0-group flatfish are the more
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14 sensitive to nursery suitability. As the duration of the wave dataset does not cover the trawl survey
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16 period (starting in 1980, Table 1), preliminary studies analyzed interannual variability of wave
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18 exposure. They showed that, at two different spatial scales (geographic sector and grid cell), this
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20 interannual variability of mean wave height from May to August was largely exceeded by spatial
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22 variability. Thus mean annual wave heights from May to August were averaged over the available 10-
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24 y period and used as a proxy for coastal exposure. Averaged wave height was split into three classes: <
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26 0.3,] 0.3 ; 0.5] and > 0.5 which correspond to a gradient between sheltered and exposed habitats.
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Non retained habitat descriptors

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33 Though water temperature is available from the 3D hydrodynamic model used to describe
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35 estuarine plume, the effect of temperature is not considered in the present study. Indeed, the focus is
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37 here on local habitat suitability for juveniles while temperature is known to drive species distribution
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39 at much broader scales (Engelhard et al., 2011). For instance, a visible effect of temperature on
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41 observed juvenile densities is more likely to reflect the spatial distribution of spawning adult than local
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43 juvenile preferences, especially for flatfish (Hermant *et al.*, 2010). In any case, the inability to
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45 distinguish the causality link may lead to spurious conclusion about temperature role on juvenile
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47 habitat suitability.
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51 Food availability is a driving factor of habitat choice (Kopp et al., 2013) and descriptors of
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53 food repartition could improve the description of habitat suitability (Stoner *et al.*, 2001; Le Pape *et al.*,
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55 2007; Nicolas *et al.*, 2007; Kopp et al., 2013). Nevertheless, exhaustive spatial knowledge (needed for
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57 mapping) on these biotic factors is not available and prevents their use for habitat mapping.
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2.3. *Coupling trawl survey data and habitat descriptors*

Shapes of bathymetry, sediment structure, salinity and wave height were included into a PostgreSQL (Copyright © 1996-2012 The PostgreSQL Global Development Group) database. Physical descriptors were temporally constant except for salinity (*i.e.* one annual map of mean salinity from January to April for each year of the study period 1980-2011). Sector limits (Fig. 1) were also inserted into the PostgreSQL database.

Survey data, identified from the mean position of the trawl haul and the year of survey were included in the database. Under PostgreSQL, the location of each trawl haul was intersected with each physical descriptor and sector information. The final dataset consisted in the 1643 selected trawl hauls, associated with the year of survey, 0-group densities for the three species, the geographical sector and the four physical descriptors.

2.4. *Modeling habitat suitability*

Model fit: the delta approach

Three separate species specific EFHS models were built on the 0-group densities. EFHS models were developed using “Salinity”, “Sediment structure”, “Bathymetry”, “Wave height” “Geographical sector” and “Year” as potential descriptive factors of suitability. Abundance indices data are typical zero-inflated data, characterized by an important proportion of zero values. Indeed the presence rates of 0-group *S. solea*, *P. platessa* and *D. cuneata* were 58.1%, 19.5% and 12.1% respectively. This non-Gaussian data distribution prohibited the use of a classical statistical approach and Delta-models were used (Stefanson 1996; Martin *et al.*, 2005; Rochette *et al.*, 2010). The Delta-model is a conditional approach coupling two sub-models: 1) a first testing for the presence; 2) a second explaining the variation of the densities in data where presence was recorded. Three steps are needed to build these models:

For each species separately, the first sub-model describes the binary presence/absence information, $Y_{0/1}$ the Boolean value of juvenile presence (1 when at least one individual from the 0-

group of the species was caught in the trawl haul, 0 otherwise) being used as the response variable.

The model is a GLM based on a binomial distribution where $Y_{0/1}$ depends upon factors through a logit link function (Eq. (4)).

$$\text{Logit}(Y_{0/1}) \approx \mu_{0/1} + F_{\text{Salinity}} + F_{\text{Sediment}} + F_{\text{Bathymetry}} + F_{\text{Wave}} + F_{\text{Sector}} + F_{\text{Year}} + \varepsilon_{0/1} \quad (4)$$

The second sub-model (Eq. (5)) uses a Gaussian linear model on log-transformed positive densities Y_+ to normalize the skewed distribution of the data.

$$\ln(Y_+) \approx \mu_+ + F_{\text{Salinity}} + F_{\text{Sediment}} + F_{\text{Bathymetry}} + F_{\text{Wave}} + F_{\text{Sector}} + F_{\text{Year}} + \varepsilon_+ \quad (5)$$

Preliminary analyses showed that this option was the best to describe the distribution of positive values (Le Pape *et al.*, 2003b; Rochette *et al.*, 2010).

Habitat suitability for each species can be estimated from the 0-group density \hat{Y} by combining the two sub-models, accounting for a correction (Laurent, 1963) to obtain an unbiased estimate of the positive densities from a linear model based on log-transformation (Eq. (6)).

$$\hat{Y} = \hat{Y}_{0/1} \times e^{\ln(\hat{Y}_+)} \times e^{\frac{\sigma^2(\varepsilon_+)}{2}} \quad (6)$$

Simple and cross-over effects were tested to choose the best model for each species. Goodness of fit (GOF) of models was evaluated based on both Chi-square tests for significance (a 5% threshold for type 1 error has been chosen for an effect to be retained) and Akaike information criterion (AIC), considered to analyze models parsimony.

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 interpreted together (Ye *et al.*, 2001). Combined (*i.e.* presence \times positive densities) mean effects have been computed to obtain relative effects of each modality of factor (Rochette *et al.*, 2010) from the following method. Predicts were generated from Eq. (6) on the modeling datasets to obtain models estimates of density for each trawl haul. For one factor, the mean effect of class c of factor f for species s is (Eq. (7)) the mean of all estimated densities on the n trawl hauls belonging to the class c divided by the overall mean estimated density on the whole dataset (1643 samples).

$$\text{Mean effect}_{s,f,c} = \frac{\sum_i^n \hat{Y}_{s,f,c,i} / n}{\sum_i^{1643} \hat{Y}_{s,f,c,i} / 1643} \quad (7)$$

Model validation

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2 As models with poor and/or biased prediction power could lead to spurious conclusions on
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4 EFHS (Planque *et al.*, 2011), their validation requires attention. In order to validate EFHS models,
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6 their GOF was evaluated comparing observed versus predicted values (Piñeiro, 2008) with a
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8 calibration/validation procedure (Vasconcelos *et al.*, 2013). Datasets of each species have been split in
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10 two parts: calibration dataset – 75% of the data – and validation dataset – the 25% remaining data.
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12 Selection was done with respect to the relative amount of data within the different classes of factors to
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14 avoid random selection bias. For each species, binomial and positive models were fitted using the
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16 calibration data set and models GOF was tested both on the calibration and the validation data sets by
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18 comparing the models predictions with data (juvenile flatfish densities). Predictions are the models
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20 fitted values for the calibration dataset and the models estimates for the validation dataset. This
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22 methodology allowed evaluating models performance. As the amount of data is lower in the validation
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24 dataset, coefficients of determination were expected to be lower for validation data. A moderate
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26 decrease in GOF from the calibration dataset to the validation dataset supports accuracy and
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28 robustness (Power, 1993; Olden *et al.*, 2002).
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33 Area Under Curve (AUC) of the Receiver Operating Characteristic (Elith *et al.*, 2006; Townsend
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35 Peterson *et al.*, 2008) was used to measure accuracy of the binomial models in predicting
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37 presence/absence. This analysis considers Boolean values correctly or incorrectly assigned (AUC of
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39 0.5 represents a useless model and AUC of 1 a perfectly fitted model).
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42 The Pearson coefficient of determination between density observed (y-axis) and predicted (x-axis)
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44 (Piñeiro *et al.*, 2008) was used to estimate the proportion of the total variance explained by the
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46 positive models.
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2.5. *Quantitative habitat mapping*

Mapping density with models predicts

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56 To sum up information on flatfish nursery habitat at the Bay of Biscay population scale, the
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58 mean distributions of the three species were mapped. For this purpose, three species specific EFHS
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60 models were fitted with the same procedure as in 2.4., without including the year effect. The effect of
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1 interannual variability was removed to build a mean habitat suitability map on which all variations in
2 0-group relative densities are solely linked to habitat features. Results of these habitat suitability
3 models were included in a GIS to map mean juvenile flatfish distribution. To do so, the mean estuarine
4 plume conditions were calculated (*i.e.* surface salinity from January to April were averaged over the
5 whole period, from 1980 to 2011) and habitat mapping was based on these average hydrologic
6 conditions. Combining the five levels of spatial information (four physical factors and one
7 geographical sector) under PostgreSQL allowed for habitat strata to be identified. A habitat stratum is
8 defined by one of the six geographic sectors, one of the four classes of bathymetry, one of the four
9 classes of sediment, one of the three classes of wave height and one of the three classes of mean
10 salinity. Thus, using PostgreSQL, a new layer was created as the result of the intersections of the five
11 shapes. This method based on vector maps respects the original resolution of each source of
12 information, to obtain a combined stratification all over the study area.

26 Model predictions were calculated for each species, providing an estimation of the 0-group
27 density with Eq. (6) for each stratum (*i.e.* each polygon). These predictions were displayed with QGIS
28 software (Quantum GIS Development Team, 2012. Quantum GIS Geographic Information System
29 1.8. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>) to produce maps.

35 *Calculating the contributions of the different habitats*

37 Predicted values of EFHS models and the GIS were combined to calculate, for each species,
38 the respective contributions of the different habitats at the scale of the Bay of Biscay management
39 unit:
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- 43 - The surface area of each stratum (Bathymetric class \times Sediment structure \times Salinity class \times
44 Wave height class \times Coastal Sector) was calculated using PostgreSQL
- 45 - For each stratum and for each species, a relative number of 0-group juvenile was calculated as
46 the product of this surface area multiplied by the corresponding density value, as predicted by
47 the delta models.

48 This relative number of fish was used to determine the contribution of the different habitats to the
49 whole stock, at the scale of the Bay of Biscay stock management unit, as a percentage of the total
50 number of fish in the overall area (Le Pape *et al.*, 2003b).

3. Results

3.1. Selection of descriptors, EFHS models fit and validation

The four descriptors of nursery habitat, the geographical sector and the interannual variability were retained as explanatory factors in EFHS models for the three species. They contribute to explain both presence and positive densities quite systematically and if not are significant in at least one of the two sub-models, except wave height in the case of *D. cuneata* (Table 2). No cross-over effect between factors was retained in EFHS models for three reasons: cross-over effects were not significant, were not retained from AIC criterion or presented singularities in some combinations that cannot be estimated because of a lack of degrees of freedom, leading to numerical bias in the estimation.

Binomial sub-models explained from 21% to 45% of the deviance in presence data, with better performance for *P. platessa* than for the two other species (Table 2). AUC indices showed great prediction accuracy of Binomial models for all species (Fig. 2 for *S. solea* and Table 3 for the three species), with moderate loss of the predictive capacity of the models between calibration and validation data.

Positive sub-models explained from 30 to 60% of the total deviance in positive densities with also better performance for *P. platessa* than for the two other species (Table 2). There were no trends in the residuals of the positive models, which confirmed that Gaussian models on log-transformed densities were appropriate to the distribution of positive densities for juvenile flatfish (Fig. 2). Similar level of performance was reached for positive models from correlations between prediction and data (Fig. 2, Table 3). The loss of predictive capacity of the EFHS models between calibration and validation was 10% for *S. solea* and *P. platessa* and lower (8%) for *D. cuneata*.

Thus, even if their power to explain variability in the data appeared limited, the delta models with six descriptive factors were adapted to the 0-inflated lognormal distribution of 0-group flatfish densities and the calibration-validation procedure demonstrated their robustness.

3.2. Effects of the descriptors on 0-group flatfish densities

1 Bathymetry was significant for presence and positive density models for the three flatfish
2 species. This factor is of major influence for *S. solea* and *P. platessa* for which it explains respectively
3 roughly 8% and 14% of deviance in both presence and positive density models (Table 2). Bathymetry
4 mean effects confirm the high influence of this factor on *S. solea* and *P. platessa* (Fig. 3), with a
5 strong predilection for shallow waters. A drop in estimated density can be observed as bathymetry
6 increases, 0-group densities in the shallower class of bathymetry being about four times higher than
7 the one of the following class (5-10 m) for both species, with a continuous decrease along the two
8 following classes of bathymetry. *D. cuneata* seems less influenced by bathymetry.
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11 Sediment type was significant in both presence and positive density models for the three
12 flatfish species. Although sediment structure is of lesser influence than bathymetry, except for *D.*
13 *cuneata*, some significant patterns are visible on Fig. 3, *S. solea* and *P. platessa* both presenting a
14 strong correlation with mud and *D. cuneata* with fine sand.
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17 The effect of salinity was also significant in the two sub-models for the three species; however
18 it appears limited as an explaining factor (Table 2). *P. platessa* shows a high affinity to estuarine
19 waters (Fig. 3), whereas it is less obvious for the two other flatfish species.
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22 Wave height was significant on both presence and positive density of 0-group for *S. solea* and
23 on the positive density for *P. platessa*, on which it is particularly influent (Table 2). Mean effects
24 reveal a predilection of *S. solea* and *P. platessa* for sheltered areas, *i.e.* areas belonging to the lowest
25 wave height class (Fig. 3). Mean effect decreases rapidly as wave height increases for both species.
26 There is no influence of this factor on *D. cuneata* distribution.
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29 Geographic sector was significant on both presence and density of 0-group for *S. solea* and *P.*
30 *platessa* while being significant only on presence for *D. cuneata* (Table 2). Geographic sector is
31 particularly effective to discriminate presence of *P. platessa* and *D. cuneata* rather than *S. solea*. These
32 two flatfishes have marked latitudinal trends (Fig. 3): from no occurrence in the Gironde to a
33 northward increase for *P. platessa*, versus a northward decrease for *D. cuneata*.
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36 Year factor significantly influences presence and positive density of 0-group for all flatfish
37 species with a larger influence on positive density than on presence. Interannual variability is lower
38 than spatial variability (spatial factors) for *S. solea* and *P. platessa*, whereas it is the opposite for *D.*
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cuneata (Table 2). Mean effects provide insights on the interannual variability and temporal trends of density for 0-group (Fig. 4). They reveal opposite trends on two studied species, *P. platessa* and *D. cuneata*. The first decreased from the late 1980s to the early 2000s whereas the latter increased over the same period.

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

High densities of 0-group *S. solea* can be found on restricted coastal areas, near river mouths or in sheltered bays (Fig. 5). The same coastal preference can be observed for *P. platessa* and *D. cuneata* although distribution of *D. cuneata* extends a little farther off the coast. For these two species, densities are lower than for *S. solea*. Opposite latitudinal trends (Fig. 3) induce opposite spatial gradients (Fig. 5), with a southern area of distribution for *D. cuneata* and a northern one for *P. platessa*.

Across the entire Bay of Biscay (i.e. at the scale of stocks management unit) the respective contributions of different habitats to the total amount of juvenile flatfish were calculated (Table 4). Shallow waters appeared essential for *S. solea* and *P. platessa* with more than 75% of the total amount of 0-group located in the shallowest class (<5m) of bathymetry, this concentration being lower for *D. cuneata*. Muddy areas mainly contribute to the total population of 0-group fish for *S. solea* and *P. platessa*, with contributions higher than 75%. On the contrary, fine sand appeared essential for *D. cuneata*. Shallow (<5m) areas covered by mud and fine sand appeared essential for the total amount of 0-group flatfish. When the three species are summed, these habitats contribute for 70% of the flatfish juvenile in the Bay of Biscay, while accounting for only 20% of the surface of coastal areas (≤ 35 m) off the Bay of Biscay. Sheltered areas (Wave height < 0.3 m) appear especially suitable, hosting two thirds (68%) of juvenile *S. solea*. Shallow sheltered areas covered by mud and fine sand represent 8% only of the coastal zone but host almost half (48%) of the total amount of juvenile flatfish, when the three species are accounted for.

4. Discussion

4.1. Relevance of the method

1
2 Marine fish abundance survey data are often zero-inflated, with associated high variability in
3
4 the remaining positive data (Stefansson, 1996). The beam trawl survey data used in the present study
5
6 display an important proportion of zeros accentuated by the selection of a particular life stage (0-
7
8 group). The delta method implemented in this study enables to process such zero-inflated data. Delta
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10 models are commonly used for 0-inflated data (Stefansson, 1996; Welsh *et al.*, 1996; Brynjarsdóttir
11
12 and Stefansson, 2004). However, the delta model presents some limits related to the correlation
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14 between the two datasets (presence-absence and positive density). Indeed, the construction of the two
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16 sub-models relies on the hypothesis that the probability of presence and the distribution of the positive
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18 catch are independent (Fletcher 2008; Calama *et al.*, 2011). However, data reveal that sites with a high
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20 probability of presence are also harboring high densities. Presence and density can therefore not be
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22 considered as independent and the bias introduced by the calculation of the estimated density as the
23
24 product of the two probabilities is unknown. Alternative methods, *e.g.* compound Poisson process
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26 (Ancelet *et al.*, 2010) or Tweedie distribution (Shono, 2008), have been implemented to analyze and
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28 solve this bias. They provided results similar to those produced by the delta method but were more
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30 complicated to implement and less parsimonious. The delta method was therefore retained as it was
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32 the most straightforward to fulfill the objectives of the study. Moreover, a main interest of the delta
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34 method is the separate analysis of the probability of presence on the one hand and the level of positive
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36 catch on the other hand. Such segregation enables a more refined analysis with different variables
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38 accounting for the two sub-models and ecological interpretations can emerge (Ye *et al.*, 2001; Le Pape
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40 *et al.*, 2004). Indeed, the present study revealed a higher influence of wave height and interannual
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42 variability on positive densities than on probability of presence. These two factors appeared more
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44 influent in modulating density than spatial extent of juvenile flatfish.
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51 A validation process separating a calibration and a validation dataset was used to evaluate the
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53 robustness of EFHS models. The prediction of responses based on new data sets provided a mean to
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55 estimate how accurate were the models predictions when using external data (Planque *et al.*, 2011;
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57 Vasconcelos *et al.*, 2013). With reasonably lower GOF on calibration data than on validation data, this
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59 procedure validated the two sub-parts of the EFHS models for the three studied flatfish species. The
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1 similarities between the model developed for *S. solea* only and a previous approach (Le Pape *et al.*,
2 2003b) also contributed to this validation. The previous dataset was upgraded with ten years of data
3 (44% of additional data) furthermore including data from the inner part of rivers, which were totally
4 new locations. Despite this tremendous change, results on *S. solea* highlighted the same general
5 patterns. This consistency can therefore be considered as another confirmation of the robustness of the
6 method and its appropriateness to study juvenile flatfish habitat suitability.
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15 4.2. *Nursery habitat suitability for S. solea: confirmed knowledge, new insights and* 16 *remaining gaps* 17

18 The preference of juvenile *S. solea* for shallow areas (Gibson, 1997) covered with fine
19 sediment was previously established (Le Pape *et al.*, 2003b). The present EFHS models–GIS coupled
20 approach confirmed that shallow (< 5 m) and muddy grounds contribute greatly to the total population
21 of 0-group from *S. solea* and can be considered as essential nursery habitats for this species. They
22 harbor nearly two thirds of the total amount of juvenile *S. solea*, while representing only 16% of the
23 overall coastal study area. Besides, locations deeper than 20 m and grounds not covered with fine
24 sediment are unsuitable as nursery grounds for *S. solea*.
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35 Coastal exposure affects habitat structure, which might influence settling behavior and
36 survival of juvenile fish. Juvenile flatfish prefer sheltered parts of the coast and embayments (Pihl and
37 Van der Veer, 1992; Howell *et al.*, 1999) and this preference was suggested for *S. solea* (Le Pape *et*
38 *al.*, 2003b). However, no parameter had previously been included in EFHS models to quantify the link
39 between sheltered places and high densities of 0-group *S. solea*. The addition of wave height as a
40 proxy of coastal exposure to explain spatial distribution in EFHS models for juvenile *S. solea*
41 quantified the significant negative influence of wave exposure on habitat suitability. Wave exposure
42 affects sediment structure, an important factor of suitability for juvenile flatfish (Gibson and Robb,
43 2000) and this could explain its influence on flatfish nursery suitability (Pihl and Van der Veer, 1992;
44 Howell *et al.*, 1999). Nevertheless, this influence was taken into account in the developed EFHS
45 models by a specific descriptor based on granulometry. By adding information to EFHS models
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1 including sediment description, the present models demonstrate that wave exposure can be considered
2 as a cause of physical perturbation on the bottom sediment for young flatfish, affecting habitat
3 suitability in addition to its effect on sediment granulometry. Indeed, wave induces currents and bed
4 stress, which can alter survival during larval settlement and metamorphosis and also nursery habitat
5 structure and complexity (Polte *et al.*, 2005), with consequences on suitability for juvenile flatfish. In
6 EFHS models for juvenile *S. solea*, this influence explains half as much deviance as the remaining
7 spatial variability (itself explained by differences between geographical sectors). Indeed, compared to
8 the results of Le Pape *et al.* (2003b) the mesoscale variability (*i.e.* Sector effect) has dramatically
9 decreased, from 11.8% (presence) and 20.9% (positive) in the previous sub-models for *S. solea* to
10 3.1% and 4.7% now, respectively. The effect of wave exposure should have been even more important
11 if the central part of the bay, between Bays of Bourgneuf and Pertuis Breton (Fig. 1), previously
12 shown as not suitable as nursery ground (Le Pape *et al.*, 2003b) and largely exposed to wave, had been
13 included in the study. Wave exposure has therefore to be considered as an unavoidable explanatory
14 variable of EFHS for 0-group *S. solea*. Shallow protected habitats are highly utilized as nurseries for
15 0-group flatfish and deserve special attention in management or conservation efforts (Fodrie and
16 Mendoza, 2006).

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However, in the present study the percentage of deviance unexplained by the EFHS model for juvenile *S. solea* reaches 79% and 68% for the presence and positive densities sub-models respectively. Four sources of remaining variability could explain this result:

- Restricted study area. In spite of the use of additional explaining factors, the proportion of variance explained by the present models was not improved with regards to the previous (Le Pape *et al.*, 2003b) approach (21% here vs 23% previously and 32% vs 29% for the presence and the positive sub-models respectively). One could consider the new EFHS model for *S. solea* as less performing with regards to its similar explained variability but lower parsimony. Nevertheless, it is important to note that the present dataset focused on nursery areas, restricted to bathymetry $\leq 35\text{m}$ (50m before) and to favorable sectors (*i.e.* excluding the unsuitable areas in central part of the Bay of Biscay). This focus on nursery sectors with lessened contrasts (between areas where 0-group catches were scarce, excluded here, to the suitable habitats included in the present study) limits the apparent explanatory

1 power of models. Due to these differences in the constitution of the dataset, the present models with
2 additional descriptors improve previous description of EFHS in spite of a similar explained variance.

3
4 - A raw description of habitat drivers. The arbitrary choice of mean surface salinity from
5 January to April to describe the estuarine plume does not reflect the local continuous ecological
6 processes (Greenwood, 2007) involved in *S. solea* estuarine dependence at juvenile stages (Courrat *et*
7 *al.*, 2009; Le Pape *et al.*, 2013). Accordingly, a better explanatory variable than sediment type in three
8 different classes could improve EFHS models (Stoner *et al.*, 2001).

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11 - Additional drivers of habitat suitability. Biotic conditions (*e.g.* food availability and
12 predation) are essential driving factors of habitat choice and could be selected considering their widely
13 acknowledged influence on the distribution of juveniles (Diaz *et al.*, 2003; Adams *et al.*, 2004).
14 Especially, descriptors of the benthic food source could contribute to significantly improve the
15 description (Stoner *et al.*, 2001; Le Pape *et al.*, 2007; Nicolas *et al.*, 2007). Habitat changes related to
16 invasive species, such as presence of *Crepidula fornicata* (Le Pape *et al.*, 2004; Kostecki *et al.*, 2011)
17 or proliferation of green algae (Pihl *et al.*, 2006; Wennhage *et al.*, 2007) could also be considered for
18 their strong negative effects. Nevertheless, exhaustive spatial knowledge (needed for mapping) on
19 biotic factors is seldom available and habitat mapping is here, and in general predominantly, based on
20 abiotic factors only.

21
22 - Estimation error. Small-scale variability occurs in patchy juvenile flatfish distribution (Allen
23 and Baltz, 1997; Rogers, 1992) and could not be reflected by sampling units covering several
24 thousands of square meters. Moreover, uncertainty in estimates related to survey conditions (Poulard
25 and Trenkel, 2007) prevent EFHS models from achieving a complete description of 0 group *S. solea*
26 densities.

27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 4.3. *Generalization to coastal and estuarine dependent flatfish species*

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53 With regards to EFHS models for *S. solea*, the present study reveals levels of models
54 performance similar for *D. Cuneata* and higher for *P. Platessa*, and comparable patterns. Dependence
55 to shallow muddy areas appears stronger for *P. platessa* than for *S. solea* in the Bay of Biscay. The
56 relationship between nursery grounds and estuarine productive areas is also supported for this species.
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1 This preference of *P. platessa* for shallow productive muddy areas at juvenile stages confirmed
2 previous observations in the Eastern Channel (Riou *et al.*, 2001), the Irish Sea (Nash *et al.*, 2007), the
3 North Sea (Bolle *et al.*, 2009) and the Baltic Sea (Wennhage and Pihl, 2001). Wave height is also
4 highly significant for *P. platessa* on positive density of 0-group and explains twice as much deviance
5 as the remaining mesoscale variability. This preference of *P. platessa* for sheltered coastal areas was
6 also previously evidenced (Pihl and Van der Veer, 1992). On the contrary, *D. cuneata* presented
7 differences in spatial distribution compared to *S. solea* and *P. platessa*. Juvenile of *D. cuneata* were
8 distributed towards deeper water and depended on sea floor covered with fine sand for nursery. Nor
9 has waves height showed significant influence on *D. cuneata* and dependence to sheltered areas cannot
10 be generalized. Distribution and habitat of juvenile *D. cuneata* are closer to these of *Buglossidium*
11 *luteum*, a smaller and non-commercial flatfish species living in less shallow soft bottoms (Amara *et*
12 *al.*, 2007). Nevertheless, locations deeper than 20 m are also unsuitable as nursery grounds for *D.*
13 *cuneata*, as were grounds covered by coarse sand, gravel and rock. Thus, shallow coastal areas can be
14 considered as EFH for flatfish, with niche contrast among species. In addition, coastal areas are
15 capable of functioning interchangeably with polyhaline estuarine regions as nursery habitat (Able *et*
16 *al.*, 2005; Kostecki *et al.*, 2012; Woodland *et al.*, 2012; Le Pape *et al.*, 2013), with interannual
17 variations related to river flow conditions (Le Pape *et al.*, 2003a; Darnaude, 2005).

18 *P. platessa* and *D. cuneata* showed mesoscale gradients linked to latitudinal trends. Their
19 abundances respectively increased and decreased as latitude increased, in response to their
20 biogeographical distribution. The Bay of Biscay is respectively the southern and northern limit of
21 distribution for these two species (Désaunay *et al.*, 2006; Hermant *et al.*, 2010). Accordingly, strong
22 temporal trends were revealed for these two species: dramatic reduction, close to disappearance, of *P.*
23 *platessa* from the early 1990s to the mid-2000s and progressive increase of *D. cuneata* from the late
24 1990s. These trends were confirmed to come from a warming of the waters in the Bay of Biscay,
25 impacting both northern (*e.g.* *P. platessa*; Engelhard *et al.*, 2011) and southern (*e.g.* *D. cuneata*)
26 flatfish oppositely (Hermant *et al.*, 2010). Both these mesoscale and temporal patterns contributed to
27 lessen the relative influence of local habitat in EFHS models for these two species, by increasing
28 contrasts between geographical sectors and along the three decades of surveys.

4.4. *From habitat suitability to coastal habitat function and management*

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2 The functionality of key fish habitats, such as nursery grounds (van der Wolfshaar *et al.*, 2011)
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4 is essential to sustain marine fish population's renewal (Iles and Beverton, 2000). More consideration
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6 should be given to the conservation of nursery habitats and their ability to sustain commercial stocks
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8 (Nagelkerten *et al.*, 2012).
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11 The present approach highlighted the usefulness of quantitative maps for management
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13 purposes. It is possible to predict geographic distributions of species by life stages from habitat
14
15 mapping approaches (Rubec *et al.*, 1999; Martin *et al.*, 2009; Lauria *et al.*, 2011). EFHS maps allow
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17 for the quantitative identification of the different habitats required for marine resources to complete
18
19 their life cycle and enable to measure their respective importance for population renewal. They may
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21 serve as input in conservation-planning approach which aims to select relevant protected areas. Habitat
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23 suitability maps constitute essential elements for prioritizing areas for conducting spatial ecosystem
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25 assessments and conservation actions (Brown *et al.*, 2000; Cogan *et al.*, 2009; Le Pape *et al.*, *in press*).
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27 By providing information needed to preserve essential fish habitats (Stoner, 2003), they may solve
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29 questions about what exactly constitutes high-value or even critical fish habitat for exploited species
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31 (Fodrie and Mendoza, 2006).
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36 The protection of restricted shallow soft bottom sheltered areas, which harbor high proportion
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38 of 0-group for estuarine and coastal nursery dependent flatfish species, appear to be a priority for the
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40 conservation of these species. They gather a large amount of the total 0-group population in a small
41
42 area and are therefore essential and effective to insure fish stock renewal (Beck *et al.*, 2001).
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46
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Table 1: Synthesis of used data (habitat descriptors and juvenile flatfish surveys)

	Spatio-temporal extent	Features	Source
<i>Physical descriptors</i>			
Bathymetry	Whole study area.	463m side grid	EMODNet Hydrography portal (http://www.emodnet-hydrography.eu)
Sediment	Study area except inner Loire.	1/500 000	Bureau de Recherches Géologiques et Minières, France
Salinity	Inner Loire estuarine area.		GIP Loire estuaire (<i>pers. com.</i>)
Coastal exposure	Whole study area. 1972-2011	4km side grid, 32 layers	ECOMARS 3D (Lazure, 2009)
	Whole study area. 2002-2011	2km side grid	PREVIMER (http://www.previmer.org/en/produits)
<i>Trawl Survey data</i>			
Vilaine	1984-1990; 1992; 1993; 1996; 1997; 2000-2005; 2008-2010	740 hauls	IFREMER; IRSTEA
Loire	1980; 1982-1984; 1986; 1997; 2000-2003; 2008; 2010	240 hauls	IFREMER; IRSTEA ; BIOLITTORAL
Bourgneuf	1981; 1982; 1997; 2000-2003; 2008	98 hauls	IFREMER
Pertuis Breton	1986; 1987; 1996; 2000-2003	140 hauls	IFREMER
Pertuis d'Antioche	1986; 1987; 1996; 2000-2003	169 hauls	IFREMER
Gironde	1996; 1997; 2000-2003; 2005; 2009-2011	256 hauls	IFREMER ; IRSTEA
All sectors combined	1980-1990; 1992; 1993; 1996; 1997; 2000-2005; 2008; 2009; 2010; 2011	1643 hauls	

Table 2

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Table 2: Analysis of deviances of Generalized Linear Models for the 3 species

a) *S. solea*

Model	Binomial				Gaussian on log (positive densities)			
	DoF	Deviance	Pr(Chi)	AIC	DoF	Deviance	Pr(Chi)	AIC
Null	1642	2235		2237	953	2694		3702
+Salinity	1640	2211	6.57E-06	2217	951	2588	3.08E-12	3667
+Sediment	1638	2140	3.91E-16	2150	949	2539	5.34E-06	3653
+Bathymetry	1635	1968	<2.2E-16	1984	946	2317	<2.2E-16	3572
+Mean wave	1633	1932	1.58E-08	1952	944	2243	8.89E-09	3545
+Geographic sector	1628	1863	1.81E-13	1893	939	2116	2.62E-12	3500
+Year	1604	1758	4.49E-12	1836	915	1832	<2.2E-16	3410
Σ explained deviance (%)		21					32	

b) *P. platessa*

Model	Binomial				Gaussian on log (positive densities)			
	DoF	Deviance	Pr(Chi)	AIC	DoF	Deviance	Pr(Chi)	AIC
Null	1386	1367		1470	269	536		955
+Salinity	1384	1303	1.16E-14	1425	267	520	1.84E-04	951
+Sediment	1382	1251	3.93E-12	1346	265	487	1.24E-08	938
+Bathymetry	1379	1042	<2.2E-16	1135	262	417	<2.2E-16	902
+Mean wave					260	373	3.65E-11	876
+Geographic sector*	1375	941	<2.2E-16	967	256	350	3.27E-05	866
+Year	1352	750	<2.2E-16	824	235	214	<2.2E-16	775
Σ explained deviance (%)		45					60	

*there is no *P. platessa* in the Gironde sector, removed from the model for this speciesc) *D. cuneata*

Model	Binomial				Gaussian on log (positive densities)			
	DoF	Deviance	Pr(Chi)	AIC	DoF	Deviance	Pr(Chi)	AIC
Null	1642	1213		1215	198	391		703
+Salinity	1640	1195	1.42E-04	1201	196	369	9.36E-04	696
+Sediment	1638	1170	2.94E-06	1180	194	350	2.61E-03	689
+Bathymetry	1635	1149	1.35E-04	1165	191	335	1.81E-02	686
+Mean wave								
+Geographic sector	1630	1105	1.76E-08	1131				
+Year	1606	945	<2.2E-16	1019	168	273	8.46E-04	678
Σ explained deviance (%)		22					30	

Degrees of freedom (DoF) and deviance are shown as residuals. Pr(Chi) are p-values from a χ^2 -test used for significance.

Table 3[Click here to download Table\(s\): Table 3.xlsx](#)Table 3 : AUC (presence) et r^2 (positive densities) of the 3 delta models

Espèces	AUC		r^2	
	Calib.*	Valid.**	Calib.	Valid.
<i>S. solea</i>	0.81	0.76	0.34	0.24
<i>P. platessa</i>	0.91	0.88	0.61	0.51
<i>D. cuneata</i>	0.81	0.73	0.32	0.25

* calibration and ** validation data sets

Table 4

[Click here to download Table\(s\): Table 4.xlsx](#)

Table 4: Relative contribution and area by class of habitat factor under mean estuarine conditions

Factor	Conditions Class	<i>S. solea</i>		<i>P. platessa</i>		<i>D. cuneata</i>	
		Contr. (%)	Area (%)	Contr. (%)	Area (%)	Contr. (%)	Area (%)
Salinity	> 32	56	51	15	41	31	51
] 30 ; 32]	24	29	38	39	35	29
	< 30	20	21	47	20	34	21
Sediment	Mud	76	48	78	56	39	48
	Fine sand	19	32	10	13	56	32
	Coarse sand	6	19	12	31	6	19
Bathymetry	> -5	78	23	81	35	38	23
] -10 ; -5]	11	18	13	17	17	18
] -20 ; -10]	8	23	6	26	35	23
] -36 ; -20]	3	36	0	22	10	36
Wave height	< 0.3	68	19	44	22	31	19
] 0.3 ; 0.5]	15	8	20	17	7	8
	> 0.5	17	73	35	61	62	73
Geographic sector	Vilaine	5	10	55	22	4	10
	Loire	6	15	17	32	2	15
	Bourgneuf	13	6	13	12	7	6
	Pertuis Breton	15	7	9	15	10	7
	Pertuis Antioche	44	9	7	19	9	9
	Gironde	17	52	*		69	52

* as there is no *P. platessa* in the Gironde estuary, this sector has been removed; contributions and surface were calculated on the 5 northern sectors

Figure legends

Fig. 1: Map of the study area showing the six investigated sectors and the trawl hauls locations (dots). In the upper right corner: general location of the study site in Western Europe.

Fig. 2: Validation of the model for *S. solea*. ROC curve on train (a) and test (b) data for *presence*. (Area stands for the AUC index); Observed log-transformed positive densities versus predicted log-transformed positive densities for calibration (c) and validation (d) data.

Fig. 3: Mean effects (0-group density of each modality over mean density of whole data, cf Eq. (7)) of the different habitat factors on the 0-group densities of the three flatfish species. Abbreviations for sediment: M=Mud, FS= Fine Sand, CS=Coarse Sand and Gravel, R=Rock. Abbreviations for sector: V=Vilaine, L=Loire, B=Bourgneuf, PB=Pertuis Breton, PA=Pertuis d' Antioche, G=Gironde.

Fig. 4: Year mean effects 0-group density of each year over mean density of whole time series, cf Eq. (7)) for the three flatfish species.

Fig. 5: Density map for *S. solea* (top left), *P. platessa* (top right) and *D. cuneata* (bottom left) and sum of the 3 species (bottom right) under mean estuarine conditions.

Figure 1

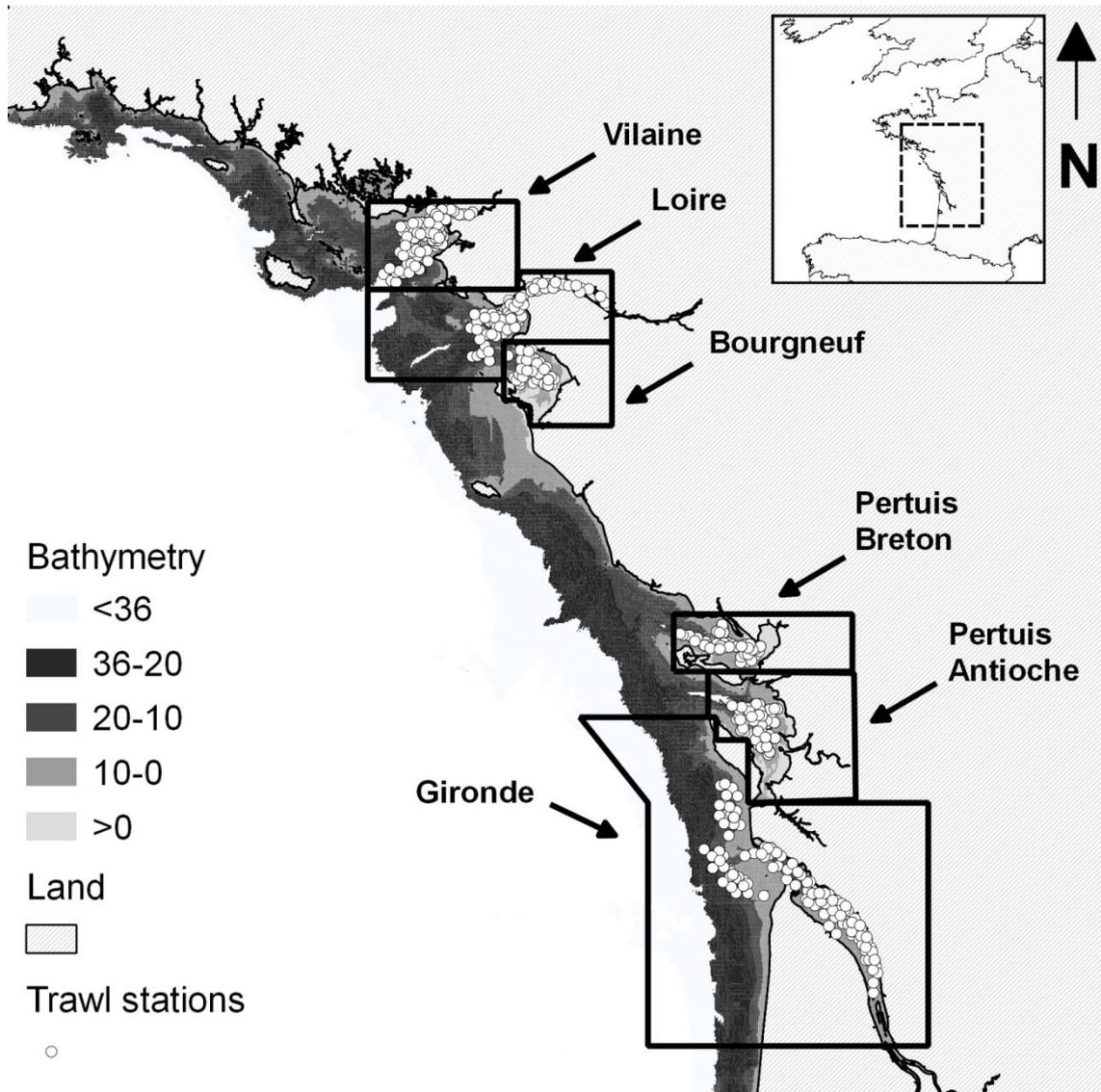


Figure 2

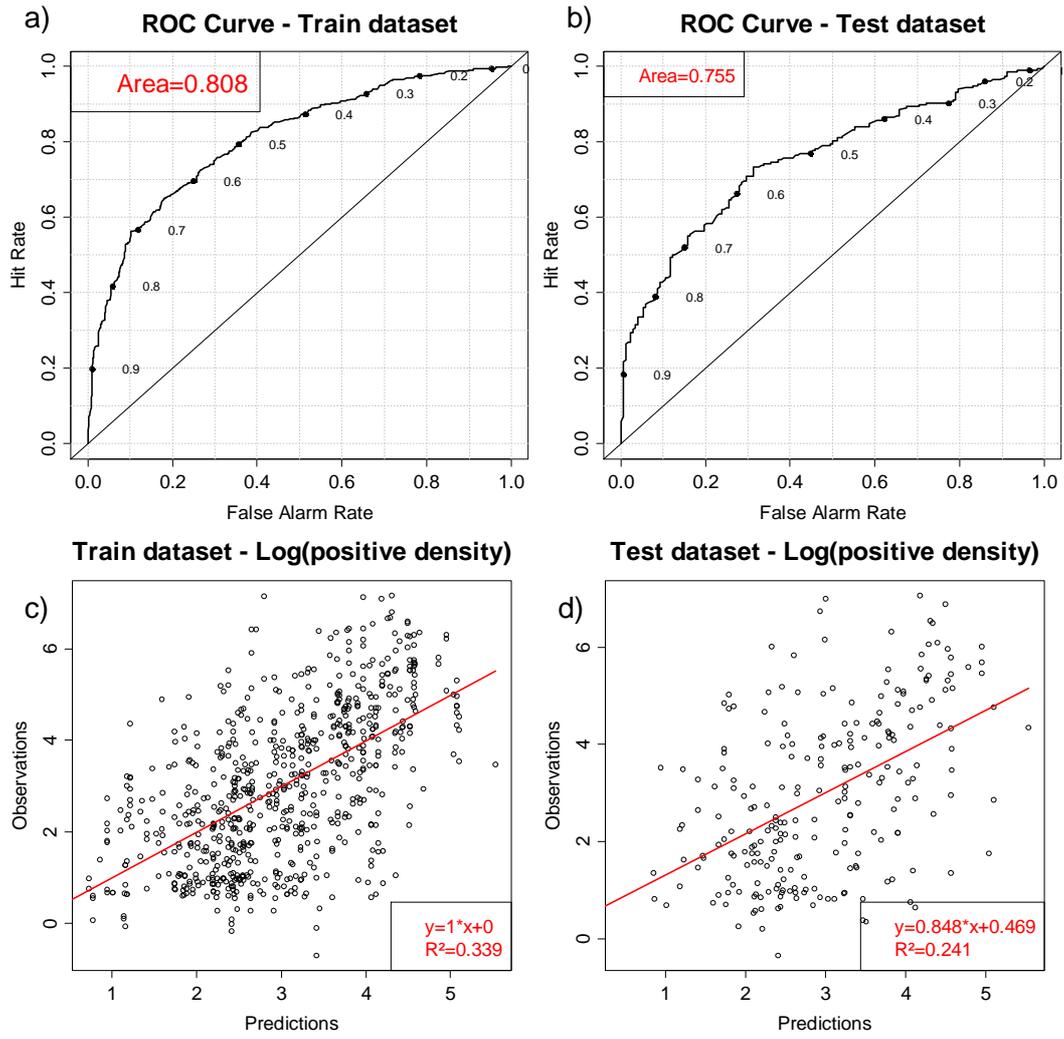
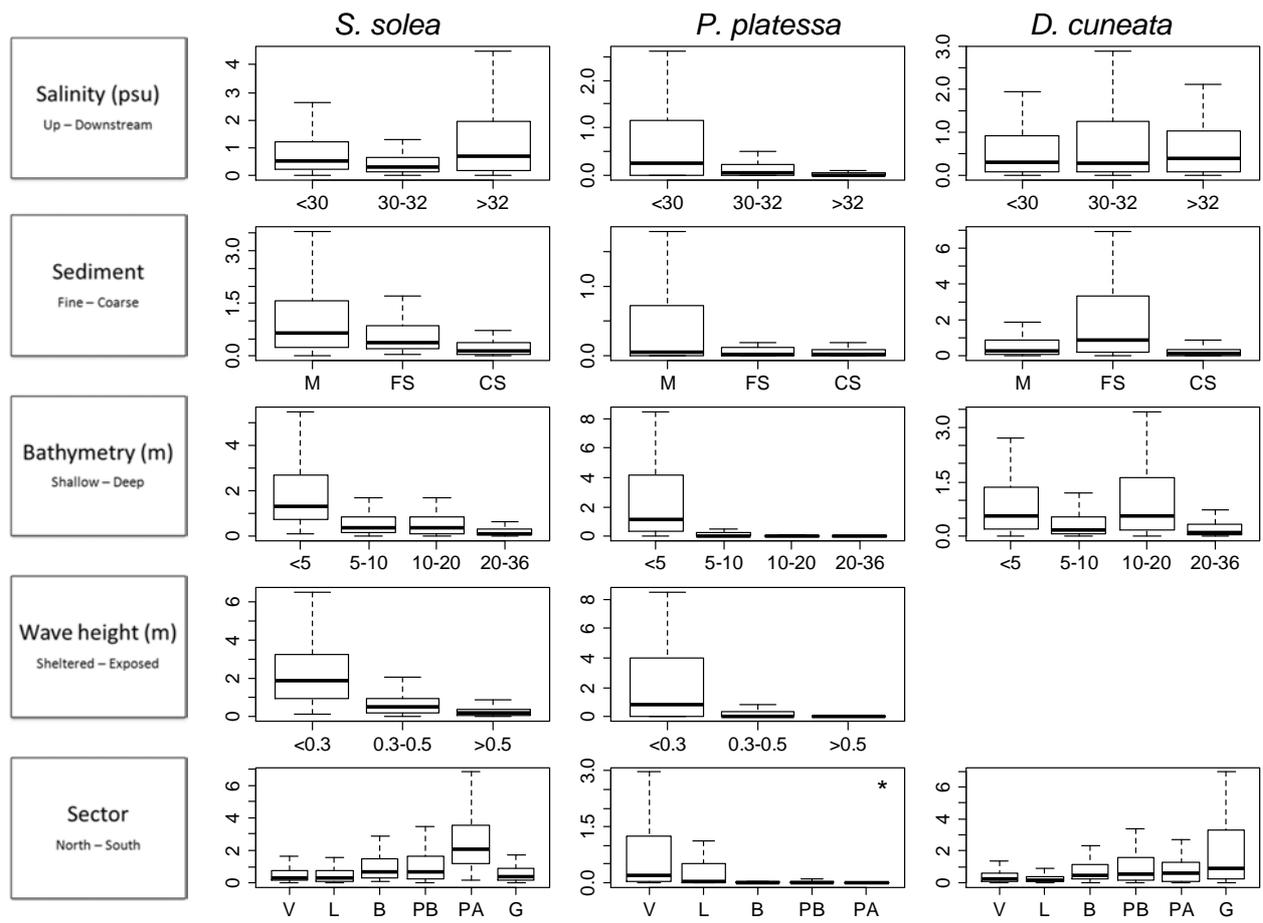


Figure 3



*there is no *P. platessa* in the Gironde sector, removed of the model for this species

Figure 4

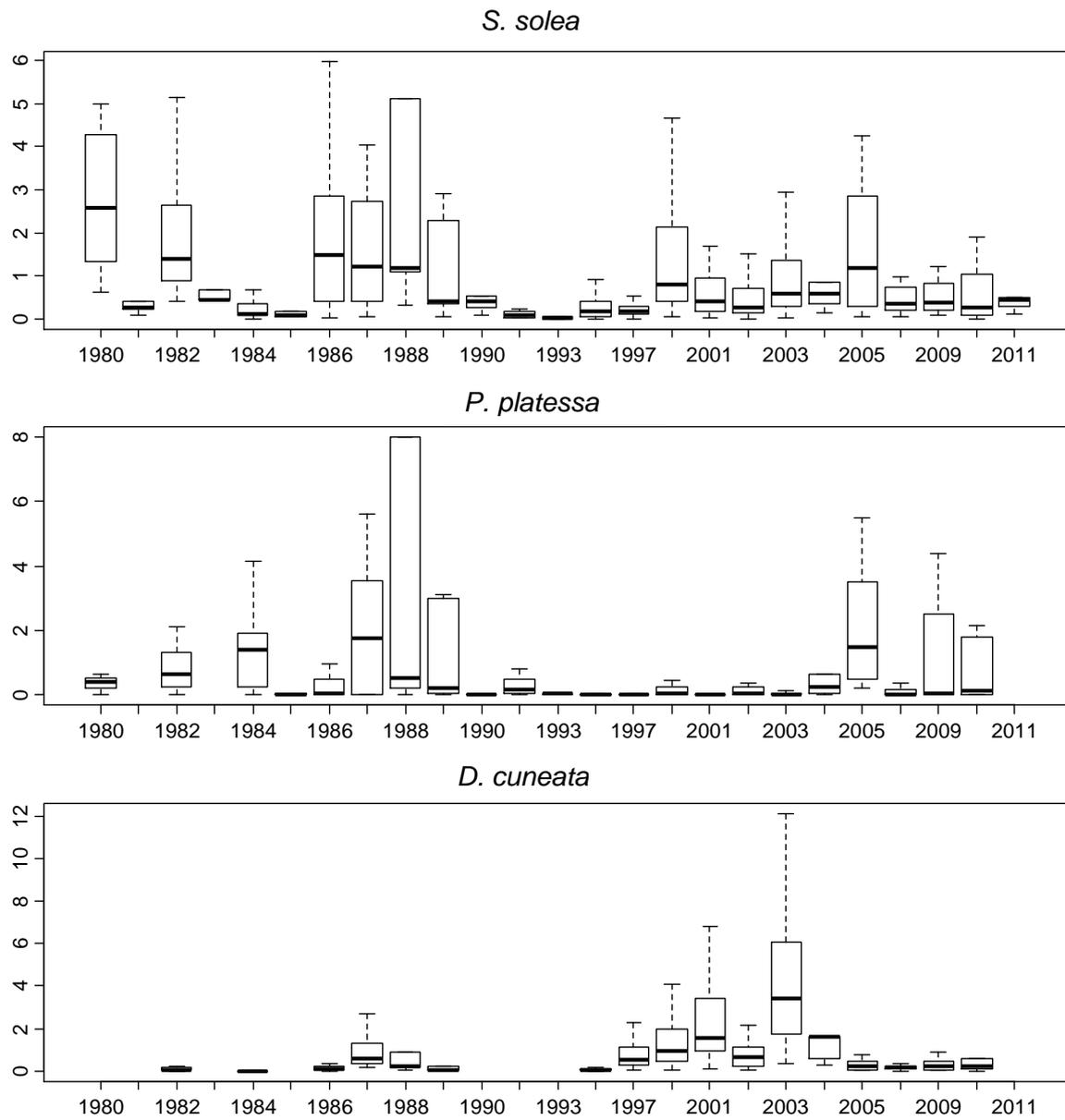


Figure 5

