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Comparison of the spatiotemporal distribution of three flatfish species in the Seine estuary nursery grounds

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A B S T R A C T

Nurseries are crucial habitats that play an important role for many marine fish species; which rely on them to complete their life cycle. Juvenile stages of dab (*Limanda limanda*), plaice (*Pleuronectes platessa*) and sole (*Solea solea*) present in the English Channel are common in the Seine estuary nursery grounds. To further explore the estuary's nursery function, we investigated the heterogeneity in spatial distribution patterns of these three flatfish at their juvenile stage, between 1996 and 2019. We used geostatistical indices and multivariate analyses to demonstrate species specific spatiotemporal dynamic. Sole favoured the most upstream part of the nursery, dab was found in the most marine areas, and plaice preferred the southern coast. We then performed clusters analysis based on spatial indices and spatial patterns extracted from a Minimum/Maximum Autocorrelation Factor (MAF). We showed that the average positions of the three flatfish species were stable across time. Each flatfish appeared to have its own spatial preference inside the nursery. No temporal variability in the spatial pattern nor trend was found that would correspond to the major stress imposed on the community by harbour development within the 2000–2005 period. We conclude that segregation of the juveniles of the three species within the nursery may reflect different ecological needs and underlying mechanisms to minimise interspecific competition.

1. Introduction

In addition to the natural variability of environmental conditions, coastal ecosystems undergo constant modifications and disturbances as human activities keep increasing (Cloern et al., 2016). A thorough understanding of the functioning of these ecosystems is needed to ensure the sustainable coexistence of human activities and of the valuable ecological services they provide (Costanza et al., 2014). Estuaries are particularly exposed to human pressure often leading to detrimental consequences on the ecosystem's functioning (Courrat et al., 2009). A function of estuaries is as nursery grounds for many fish species (Vinagre et al., 2008). They are characterised by larger biomasses of juvenile individuals in comparison to other habitats (Beck et al., 2001) and are key habitat for benthic invertebrates (Etherington and Eggleston, 2000) which provide abundant food resources to sustain juvenile fish growth (Seitz et al., 2005). Trophic resources combined with protection against predation from shallow depth (Gibson et al., 2002), large fluvial discharge increasing food availability and growth (Le Pape et al., 2003), and high productivity strengthening recruitment (Correll, 1978) make estuaries favourable.

Most flatfishes found along the French coasts are of commercial value (Hermant et al., 2010) or can be used as indicators of habitat quality (Amara et al., 2009). The Seine estuary, located in the eastern English Channel, is a nursery for at least ten species, including the three species of flatfish in this study (Duval, 1985). This area is also considered as one of the most polluted estuaries in France, recording one of the highest concentrations of PCBs in mussels for 2006, compared to other regions of the globe (Minier et al., 2006). It has been the site for several harbour developments during the 20th century, with the most recent – Port 2000, le Havre – ending in 2005 (Dauvin et al., 2010). These developments led to the loss of nursery function effectiveness (Le Pape et al., 2007), which for sole (*Solea solea)* was evaluated to a 42% decrease of its capacity (Rochette et al., 2010).

Understanding the impact of human development on the estuary nursery function for flatfishes has generated abundant literature (Riou et al., 2001; Amara et al., 2007; Rochette et al., 2010; Archambault et al., 2018). Most of the cited literature did not address spatial heterogeneity although fine-scale differences in trophic functioning have

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been described (Tecchio et al., 2015). By modelling food webs in six spatial compartments, they found functional distinctions in the different habitats and pointed out that the estuary was spatially more complex than previously thought. Moreover, it is demonstrated in another temperate estuary that competition for specific food resources is one of the main drivers of juveniles' distribution (Tableau et al., 2016). These findings motivate further work on small scale nursery usage and potential biotic interactions between different flatfish species (Amara et al., 2001; Rooper et al., 2006).

Previously, general additive models (GAMs) were applied to build habitat suitability models of flatfish in the Baltic sea (Florin et al., 2009) and for sole in the Seine estuary (Rochette et al., 2010). However, geostatistical methods are increasingly being considered in spatial ecology as a tool to improve the management of marine resources (Ciannelli et al., 2008) and account explicitly for autocorrelation between observations. Spatial eigenfunctions were applied to analyse spatiotemporal processes. These spatial eigenfunctions proposed by Griffith and Peres-Neto (2006) include methods that use eigenvectors of spatial matrices. A geostatistical version of spatial eigenfunctions is the Minimum/Maximum Autocorrelation Factors (MAFs) and was developed by Switzer and Green (1984). It was previously applied to fisheries to analyse spatiotemporal data on sardine eggs in the Bay of Biscay (Petitgas et al., 2020). Although geostatistics address spatial autocorrelation in the data, they may not explain species-environment

relationships (Ciannelli et al., 2008). Observed spatial patterns are the manifestations of underlying ecological relationships. This property of ecological spatial patterns allows us to focus on the spatial processes alone, leaving aside the environmental parameters.

The present study focused on the quantification of the spatial processes at work in the Seine nursery for juveniles of three flatfish species, dab (*Limanda limanda*), plaice (*Pleuronectes platessa*) and sole, over thirteen non-consecutive years. Using MAFs and geostatistical indices, we studied these species distributions in the nursery and if they changed following harbour development. Restoring the quality of the nursery would require a better comprehension of the ecosystem and the different pressures that weigh on it. We discussed our results on the key characteristics of both spatial patterns and temporal variability of juveniles' distributions in the Seine estuary in relation to biological traits of the species and to ecological processes.

2. Material and methods

2.1. Data collection

The analyses focused on the NOURSEINE scientific surveys dataset (Cariou et al., 2020a). The surveys aimed at describing the juvenile fish populations and exploring the Seine estuary's ecosystem functioning. They took place over 13 non-continuous years (1995–2002, 2008–2010
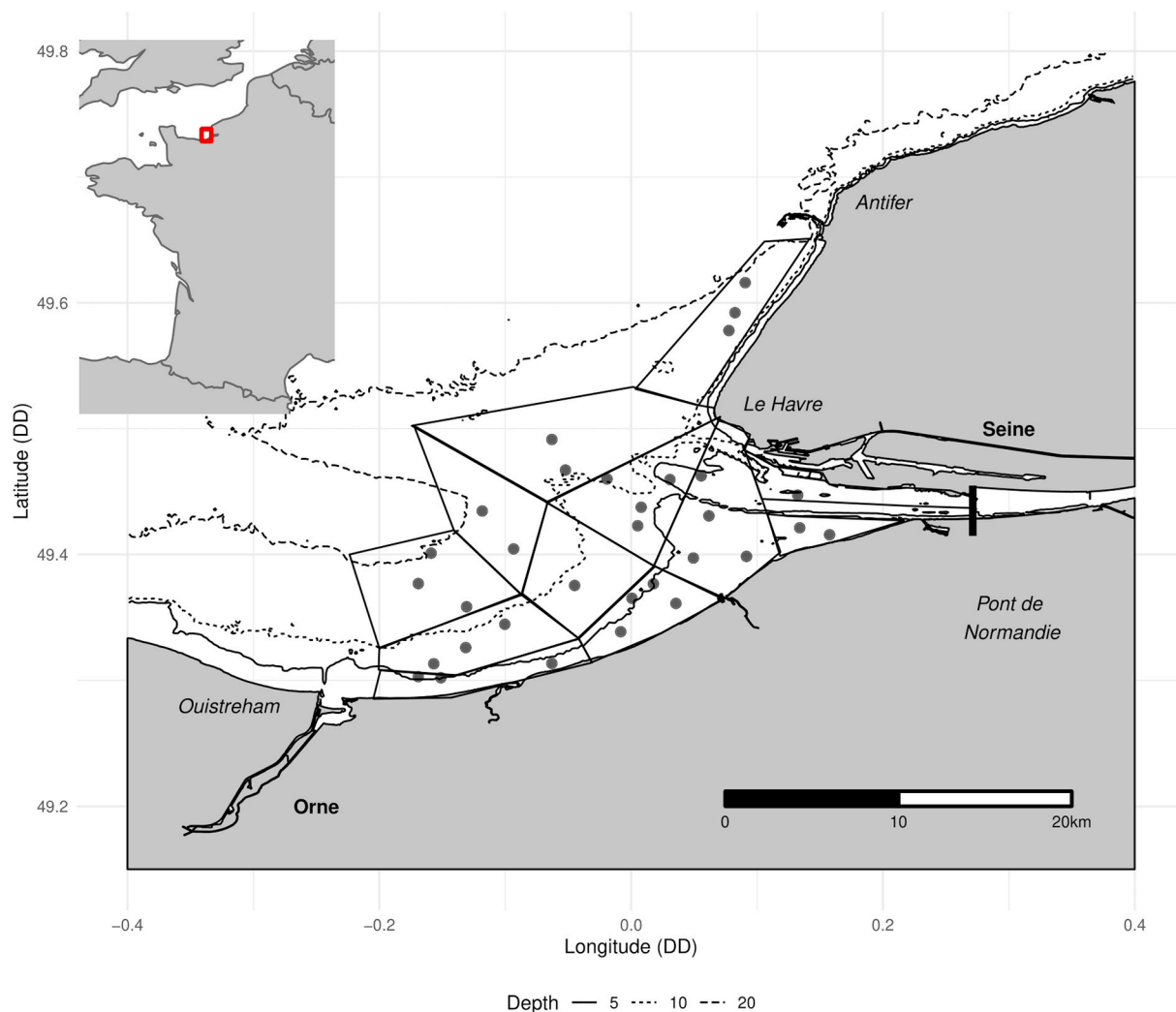
Fig. 1. Study area of the NOURSEINE survey displaying the mean position of hauls that have been performed each year. Sectors were originally established with the distance to the estuary and the bathymetry. Rivers are in bold font, cities and locations named in the article are shown. Coordinates are in decimal degree (DD).

and 2017–2019). The sampling area extended from Ouistreham (WGS84 49°17′N, 0°16′W) to Antifer (49°40′20″N, 0°11′21″E) and from the Pont de Normandie (49°26′09″N, 0°16′28″E) to roughly a 20 m-depth offshore to the west (Fig. 1). This 20 m-depth limit defines the area considered as the nursery grounds. The sampling protocol is described in Cariou et al. (2020b) and the data supporting this study are freely available on the Zenodo repository 10.18142/244 (Cariou et al., 2020a).

Dab, plaice and sole were selected for this study due to their economic importance and the availability of data to ensure robust analyses. Only records of the G0 (young-of-the-year) age group were kept, corresponding to dab of 10 cm or less, plaice of 17 cm or less and sole of 14 cm or less. These limits were defined using the size distribution of G0 juveniles, with further age determination obtained from otolith readings on a sub-sample of each species. We assumed that the G0's movement is limited. This ensures that the patterns examined reflect their distribution of the nursery.

Sample locations that were close together among years were averaged to get a spatially consistent time series of observations (Table A1). This eventually led to 32 points that were sampled systematically over the study periods (Fig. 1). The 1995 survey was removed as its sampling area was reduced and would only have 21 sampling sites.

2.2. Geostatistical indices

Summary spatial statistics were used to describe the temporal changes in spatial distributions. Four commonly used indices were applied in this study: the centre of gravity, the inertia, the global index of collocation and the local index of collocation (Bez and Rivoirard, 2001; Woillez, 2007).

The centre of gravity (CG) is the mean position of a population and the inertia describes the spreading of the population around it. These statistics were estimated by discrete summations over sampling locations with areas of influences used as a weighting factor. The area of influence of each sample was defined by all the pixels that were closer to them than to other samples. For the sample i, let s_i be the area of influence, x_i its geographical coordinates and z_i its fish density. The centre of gravity and the inertia were estimated by:

$$CG = \frac{\sum_i x_i s_i z_i}{\sum_i s_i z_i} \quad (1)$$

$$I = \frac{\sum_i (x_i - CG)^2 s_i z_i}{\sum_i s_i z_i} \quad (2)$$

The inertia was then decomposed into two principal axes orthogonal to each other, one for the maximum inertia (I_{max}) and the other for the minimum (I_{min}). It was graphically represented by an ellipse centred on the centre of gravity with axes equal to the principal axes of inertia. The isotropy index ranged between 0 (anisotropy) and 1 (isotropy) and was calculated by:

$$Isotropy = \sqrt{\frac{I_{min}}{I_{max}}} \quad (3)$$

For each species, the global (GIC) and the local (LIC) index of collocation (Bez and Rivoirard, 2001) measured the similarities in the spatial distributions between pairs of years. The GIC measures how two distributions were spatially close to each other by considering the distance between their CG relatively to their associated inertia:

$$GIC = 1 - \frac{\Delta CG^2}{\Delta CG^2 + I_1 + I_2} \quad (4)$$

When the GIC equalled 0, populations are both concentrated in a single point ($I_1 = I_2 = 0$) at different locations ($\Delta CG^2 > 0$). When CG were located at the same location, the GIC equalled 1. Between those two extremes, the GIC measured the overlap between ellipses, summarising the two distributions. However, a GIC closer to 1 did not mean that the

distributions were the same. Instead, it meant that the mean positions were very close despite their inertia. Therefore, GIC quantified global changes of spatial distributions between two selected years for a given species.

The LIC complements the GIC with station-by-station pairwise comparisons. Denoting z_{1i} and z_{2i} the fish densities observed at sample i in two different years respectively, it was estimated as:

$$LIC = \frac{\sum_i s_i z_{1i} z_{2i}}{\sqrt{\sum_i s_i z_{1i}^2} \sqrt{\sum_i s_i z_{2i}^2}} \quad (5)$$

A LIC equal to 0 indicated that the two populations never occur at the same sampling locations, while a LIC equal to 1 meant that the rank of the densities in both years are similarly distributed. In between these limits, the LIC was used to evaluate the similarity of the densities (observed at the same station) for a given species between two different years (not necessarily consecutive ones).

Calculation of GIC/LIC indices for all pairs of surveys generated square similarity matrices, opening the possibility to analyse them as networks of years. For each species, the choice was made to consider multiplex networks (Mucha et al., 2010) based on their GIC and LIC values. Whereas simple network links nodes according to their relation from a given variable, a multiplex network is a multivariate version, accounting for the relation given by more than one variable. Both GIC and LIC indices were then combined to cluster years. Years (nodes) were clustered using the Louvain algorithm (Blondel et al., 2008) that searches for the partition that maximises the modularity of the partitioned graph. The modularity (Newman and Girvan, 2004) is based on the difference between the fraction of connections that effectively connect groups and the fraction expected under random connexions between groups. To emphasise the information in the networks, only the 50% most values edges are displayed on each layer of the multiplex network, values being given by the GIC and LIC indices.

2.3. Spatio-temporal decompositions (Minimum/Maximum Autocorrelation Factor - MAF)

Principal component analyses (PCA) generally produce uncorrelated variables (also called factors) by the linear combination of the input variables and then select a reduced number of factors that explain as much as possible of the initial variability. In spatial statistics, MAFs (Switzer and Green, 1984) proceed similarly but work on spatial distributions rather than variables. A MAF procedure aims thus to explain a time series of spatial distributions by a small number of uncorrelated spatial distributions (also called factors produced by linear combinations of the input spatial distributions). Each one of the uncorrelated factors is a linear combination of the input spatial distributions. As in PCA, there are as many factors as input spatial distributions, with decreasing contribution to the overall spatial pattern. For a given species, this led to the following framework:

$$z_{i,t} = m_t + \sum_{k=1}^{13} c_{k,t} \chi_{k,i} \ , \ \forall \, t = 1, \ldots, 13, \ \forall \, i = 1, \ldots, 32 \quad (6)$$

$z_{i,t}$ denotes the fish density at sample i and year t, for $i = 1, \ldots, 32$ and $t = 1, \ldots, 13$. $\chi_{k,i}, k = 1, \ldots, 13$ are the factors of the MAF decomposition, i.e. spatial distributions that are mutually uncorrelated (at least at short distance). m_t represents the mean density of tth survey and $c_{k,t}$ represents the score of the kth MAF in the tth survey. Each MAF being a spatial factor, it is possible to build the variogram associated with the structure. The second step of the MAF decomposition allowed selecting only the most important factors to remove those associated with pure noise. Structures of the variograms were investigated only to keep those displaying the most explicit spatial structure. This led to the selection of the first three MAFs for each species (see 'result' section) so that the MAF decomposition was finally defined as:

$$z_{i,t} = m_t + \sum_{k=1}^{3} c_{k,t} \chi_{k,i} + \varepsilon_{i,t}, \ \forall \, t = 1, \ldots, 13, \ \forall \, i = 1, \ldots, 32 \qquad (7)$$

where $\varepsilon_{i,t}$ represents an uncorrelated random variable with 0 mean (pure noise).

The inference of such a model was described in details in the literature (Switzer and Green, 1984; Desbarats and Dimitrakopoulos, 2000; Woillez et al., 2009; Petitgas et al., 2020).

Each survey could then be positioned in 3-dimensional space; with "coordinates" equal to their scores in the MAF decomposition. Yearly distributions' scores on the selected MAFs were used to cluster surveys with similar spatial patterns. Clustering was based on Ward's algorithm. Simple Structure Index (SSI) was used afterwards to optimise clusters definition with regards to their intra and inter-cluster variances.

All analyses were performed using the R software, version 3.5.3 (R Core Team, 2020). Geostatistical analysis were made in RGeostats version 12.0.1 (MINES ParisTech/ARMINES, 2020); figures were made with ggplot2 version 3.3.0 (Wickham, 2016); graphs were built with ggraph version 2.0.2 (Pedersen, 2020a), igraph version 1.2.5 (Csardi and Nepusz, 2006) and tidygraph version 1.2.0 (Pedersen, 2020b); clustering used the ggdendro package version 0.1.22 (Vries and Ripley, 2020) and the SSI index was extracted from vegan version 2.5–6 (Oksanen et al., 2019). Clustering with hclust used the "ward.D2" method to use the ward criterion (Murtagh and Legendre, 2014). All codes are available on a GitHub repository (https://github.com/Thibau ltCariou/CG_MAF_FlatfishSeine).

3. Results

3.1. Mean statistics and distribution

The G0 juveniles of each species within the flatfish assemblage had different distributions patterns and abundance (Table 1). Dab and plaice were found across more than half of the total hauls. While occurring in a little more than a third of the hauls (35%), sole had the highest mean density. Map of mean distributions (Fig. 2) showed species-specific patterns. Dab was found at least once in every station, while plaice and sole were absent in some areas during the entire sampling period.

3.2. Spatial variation

Over the last 25 years, the mean position of the G0 juveniles changed for each species while remaining distinct between species (Fig. 3). The centres of gravity for dab distributions spread in the north-western part of the estuary relative to plaice and sole, except for the 1996 centre of gravity, which was located in the southernmost part of the estuary. The centres of gravity of plaice spread along the southern coast. However, two groups of ellipsis were identified at a closer look at their distribution. One coincided with the centres of gravity of sole while the other was closer to the Orne estuary (Years of each CG noted in figure A4). Sole was mostly concentrated at the mouth of the Seine estuary and had the smallest inertia on average across species. In most cases, the dispersion of individuals around the centres of gravity is not isotropic, as shown by the low isotropy index.

Table 1
Mean frequency of occurrence and density of three flatfish populations surveyed in the Seine estuary during the 13 years of sampling. C.V is the coefficient of variation.

Species	Occurrence in all hauls (%)	Density (individuals per hectare) when excluding absence	
		Mean (ind/ha)	C.V. (%)
Dab	56.2	36.7	158
Plaice	53.6	25.1	160
Sole	35.4	43.6	176

All species displayed an average isotropy index of around 0.4, indicating anisotropy. The inertia ellipsis showed that the direction of this anisotropy was species specific, and similar across years for a given species. The coastline affected the inertia along the southern coast (mainly for plaice). The main axis of inertia for dab was aligned with the isobaths in most cases. No temporal pattern emerged from the inertia or isotropy results. However, the inertia seemed to increase when the isotropy index decreased for plaice (Pearson's r: t = -4.78, df = 11, p-value = 0.00057, cor = -0.82. Normality checked with Shapiro-Wilk normality test). The inertia of plaice and dab were similar, while those of sole were significantly smaller as reflected by the small ellipsis, showing a smaller spread of the distribution around the centres of gravity (Fig. 3). The mean GIC for the three species were large (above 0.8, Fig. 4 and A.1), indicating reasonable temporal stability of the mean location for these species in the Seine estuary, relative to their spreads. For the three species, GIC values were higher than the LIC index. Hence, each flatfish population was on average observed at the same places in the Seine estuary. However, the distribution of individuals is mostly different in time. Sole had the highest contrast between high GIC and low LIC values. Although the centres of gravity were very close to one another (except for 2019), the densities distribution between the years was very different, with varying hotspots' locations through time.

The Louvain clustering detected two main clusters for each species. Dab and sole have highly connected GIC nodes, and clusters were more distinct on the LIC layer of their respective networks. Conversely, the two clusters were easily identifiable on the plaice GIC layer. No temporal similarity was found between the three clustering results in each network. The distributions of dab in 1996, 2001, 2009 and 2017 had low values of LIC, and 1996 and 2001 also having low GIC values. The lack of edge connecting these years to the others indicated that they displayed a distinct distribution. The LIC layer showed that sole exhibited a few different yet repeating patterns despite the overall LIC values being low. Four pairs of years had very high LIC values (above 0.8) showing high spatial correlations in the densities these years. However, the global signal of the LIC layer shows that the densities distributions were quite variable, with only 1997 being well connected. It is notable as well that 2019 is isolated in the GIC network.

The two clusters on the plaice network were distinguishable on both the GIC and the LIC layers. They represent the two patches of centres of gravity described in Fig. 3 and A.4. The 1996/1999/2000/2002/2017 cluster matches the centres of gravity closer to the Orne estuary, while the other contains the centres of gravity near the mouth of the Seine river.

3.3. Spatial structures

Based on the eigenvalues and the shape of each MAF variogram, only the first three MAFs were considered (Fig. 5). The variograms indicated clear structure until the third MAF, where they started to present a large nugget component. After the third MAF, the orthogonality at short distances was also not verified anymore. These three MAFs displayed spatial patterns at the estuary scale, as shown by the MAF scores shown on the map in figure A2.

The SSI index discerned 5 clusters for each species (Fig. 6). The clusters of each species did not display clear temporal continuity. Dab's clusters displayed three singletons (1996/1997/2001) whereas most sole's clusters had group membership of two or three years. As seen in the GIC/LIC clustering, the temporal dynamics for each flatfish was different. However, for dab and plaice, the most recent years tended to be grouped together (2017/2018 for dab and 2018/2019 for plaice).

4. Discussion

4.1. Methods

In this study, spatial indices and multivariate analyses were used to
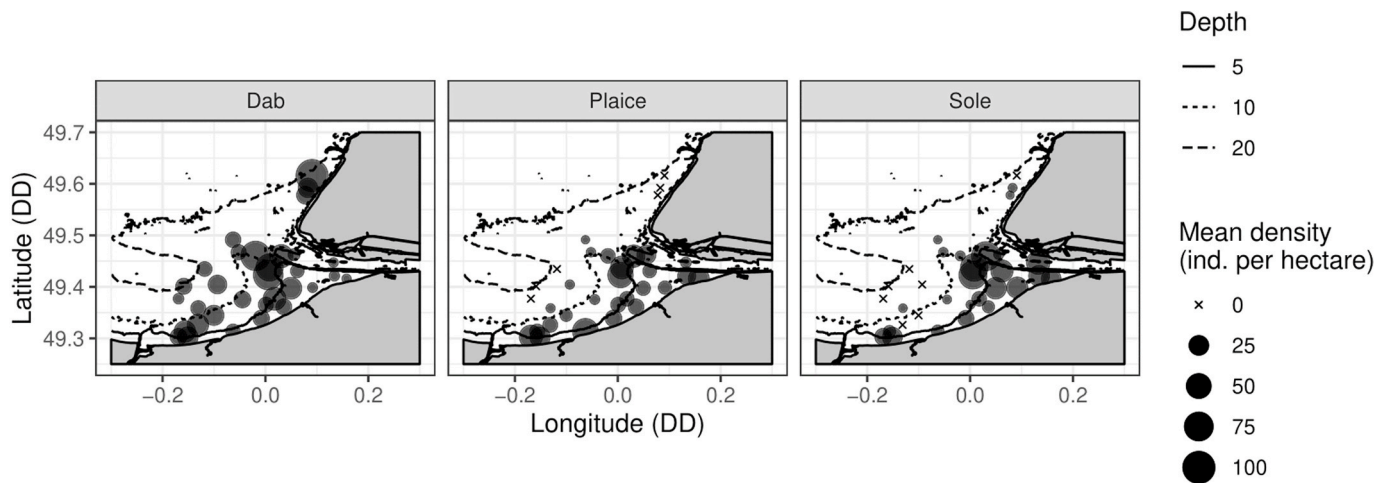
Fig. 2. Mean density of dab, plaice and soles across all surveys and hauls, between 1995 and 2017. Density is expressed in individuals per hectares. Coordinates are in decimal degree (DD).
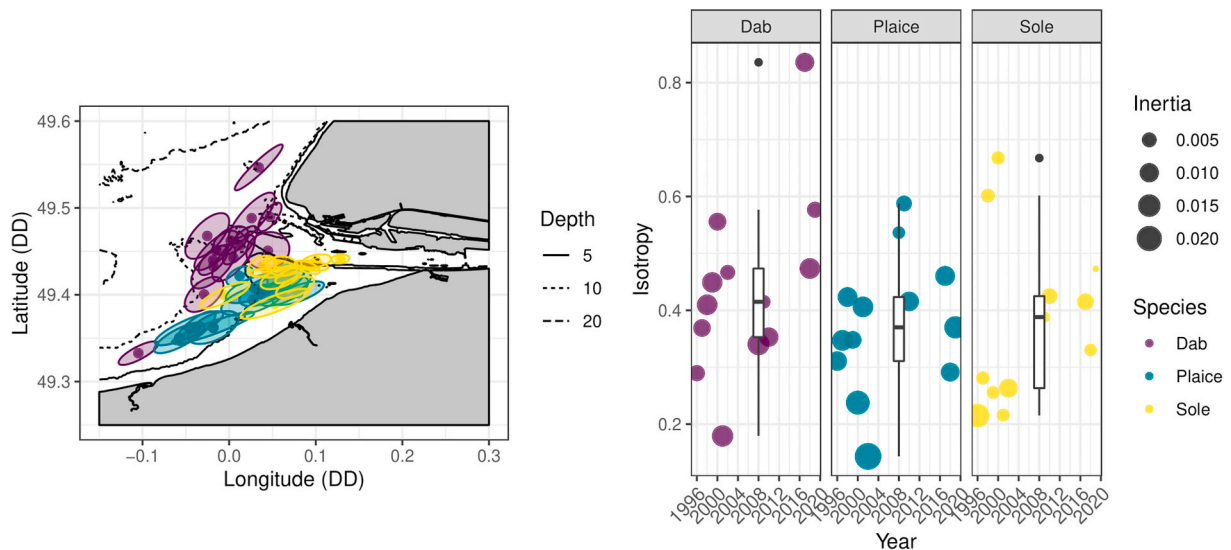

Fig. 3. (Left) Position of the centres of gravity across years for dab (violet), plaice (turquoise) and sole (yellow). The ellipsis represent inertia associated with the centre of gravity. (Right) Boxplot and annual isotropy index for the three species of flatfishes. The size of the symbol for the annual isotropy is proportional to the inertia. Coordinates are in decimal degree (DD). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

describe quantitative spatial patterns and to evaluate their temporal variation. Both methods were well suited to deal with the temporal discontinuity existing in the dataset. The spatial indices provided information on how a population was distributed or how the distributions of the two populations looked alike. A missing year would only result in not having the information on the distribution and not introduce any bias. MAFs were a k-table analysis, a table being the densities of the three flatfishes for one survey. These tables could be switched in the analysis without changing the results as the PCAs were not affected by the relative order of the values. Therefore, thirteen years of surveys provided a non-continuous yet informative dataset on G0 juvenile flatfish distributions in the Seine estuary. However, the temporal discontinuity may have altered our ability to detect any dynamic trend in spatial patterns.

Here, the combination of spatial methods and the comparison of their results allowed us to better read the spatial patterns existing in the estuary. On one hand, the considered spatial indices acted as indicators, numerically summarising distributions. On the other hand, MAFs were closer to a model of the actual distribution, removing noise in the spatial

patterns (Petitgas et al., 2020). Temporal variations in flatfishes' distribution in the Seine estuary existed but may be too faint to be rendered correctly by spatial indices. CG, inertia and indices of collocation were global statistics, which smoothed the temporal aspect of the distribution. In this study, they tracked major changes but were less able to render short term variations. Only the LIC layer of the multiplex network gave an insight into annual variability, based on the Louvain clustering algorithm. This algorithm was selected because of its widespread use and appropriate properties (Traag et al., 2019), which were considered sufficient for the objective of this study: interspecific comparison of spatiotemporal distribution. Strictly speaking, LIC is not a spatial statistic as it is unchanged by a geographical permutation of the observation. Clusters of years based on the GIC/LIC, and the clusters extracted from the spatial analysis based on the MAF decompositions were not similar. For instance, the year 1996 for dab would instinctively be isolated from the clusters detected when based on the LIC, but this was not the case with the Louvain clustering. It was considered that MAFs were better suited to track temporal changes in spatial distributions: spatial indices summarised the spatiotemporal variations in a single value,

Dab
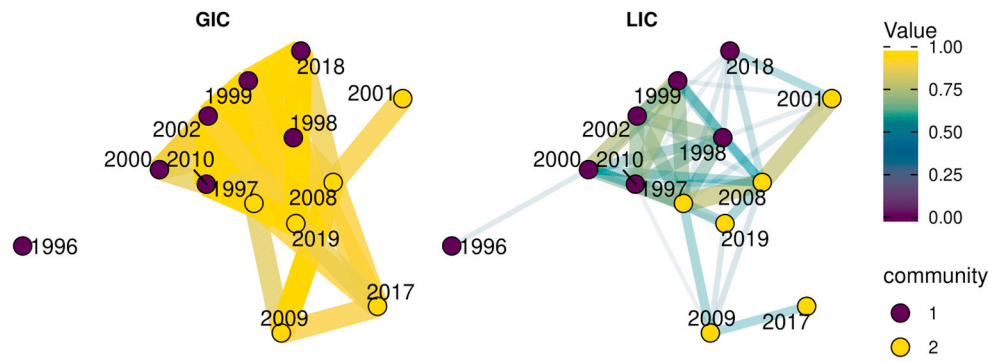
Plaice
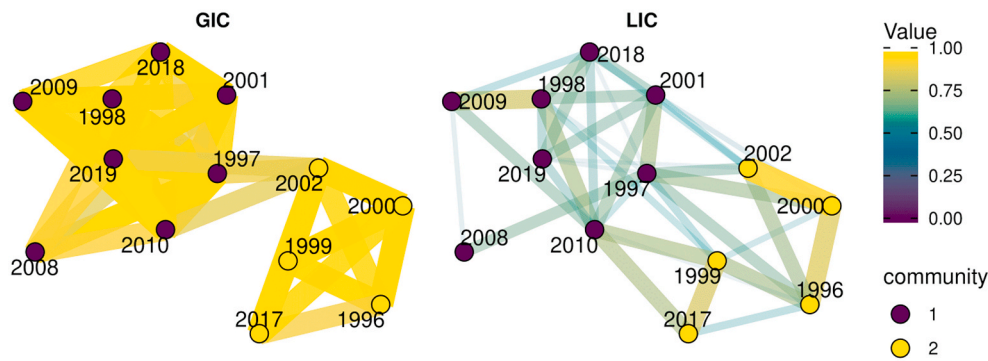
Sole
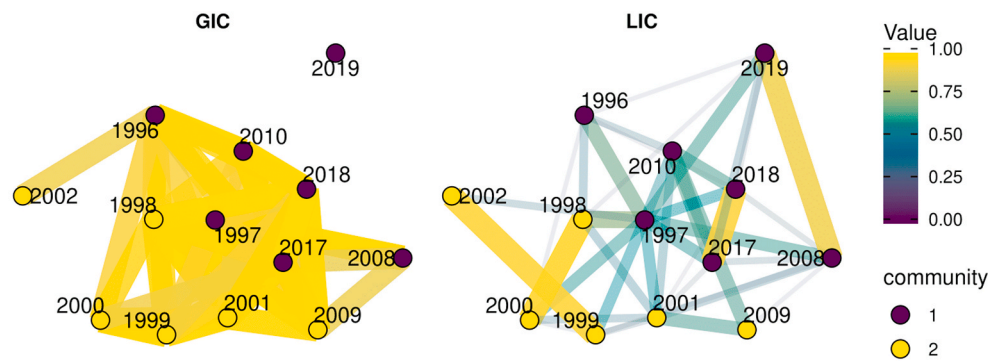
Fig. 4. Global index of collocation (GIC) and Local Index of collocation (LIC) calculated for any pair of years for the three flatfish species. A community is a synonym for a cluster. Node clusters are obtained through the Louvain algorithm, optimising the modularity of the multilevel network. The edges' thickness of the network is proportional to the value of the GIC or LIC index. On each layer, only the edges whose weight are greater than the median of all values are shown (50% of edges are removed from each layer).

while scores of the orthogonal factors for each year could group them according to coherent spatial structure. Tableau et al. (2016) used part of the analytical tools of this study (GIC and variogram) to link the distributions of preys and fishes in an estuary without describing the spatial use of the environment at the species level.

4.2. Distinct usage of the nursery in spatial patterns

The Seine nursery is a key habitat in the life cycle of the three flatfish species. It is under pressure from human activities that undermine its role as a nursery (Le Pape et al., 2007). So far, associated studies mostly focused on sole population (Amara et al., 2007; Rochette et al., 2010), and to a lesser extent on flounder (*Platichthys flesus*) and dab as indicators of pollution levels (Amara et al., 2009; Dévier et al., 2013). Plaice was studied in the Seine estuary in Riou et al. (2001) and most recently in Day et al. (2020) who analysed the feeding habitat of plaice and sole juveniles. Our study was, to our best knowledge, the first attempt to look for different spatial patterns in the Seine estuary's flatfish assemblage. Although only three species were considered in this study, the spatial indices and the MAF all pointed out segregation of the distribution of the juvenile flatfish. It showed a distinct species-specific usage of the nursery area. Similar results were obtained by Piet et al.
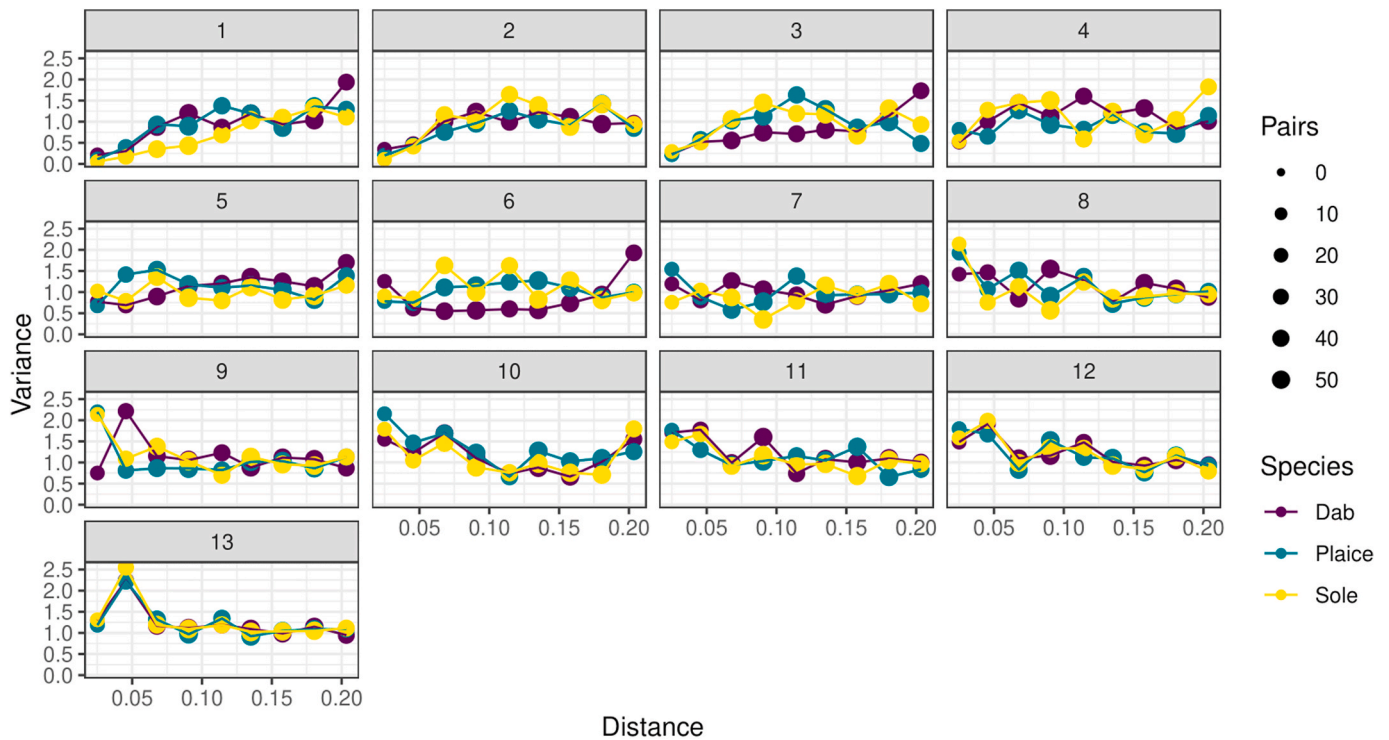
Fig. 5. Empirical variograms of each MAF for the three species of flatfish.

(1998), who worked not only on juveniles but on all size classes. They found a difference in spatial distribution between dab, plaice and sole that were significantly more distinct for the smallest size class than the largest ones found in the southern North Sea. They linked this segregation to several hypotheses revolving around trophic resources. Several studies conducted on flatfishes in the Seine estuary showed a resource partitioning in their diets (Amara et al., 2001; Dauvin et al., 2012; Day et al., 2020). They tended to indicate that trophic competition between dab, sole and plaice was minimal. A comparison of the gut contents between sole and plaice in 2017 demonstrates a high site fidelity within nursery habitats for both species (Day et al., 2020), which is consistent with our results on the relative stability of distributions' mean position across the years. As each species has environmental preferences, the spatial pattern we highlighted in the estuary may be related to different nursery environments (Peterson et al., 2011).

Dab juveniles in the Seine estuary are recurrently found in the furthest western and northern parts (Fig. 2). The literature on this species in other ecosystems and the English Channel showed that dab juveniles did not just use the shallow and estuarine areas as nursery grounds but may use deeper waters as well (Bolle et al., 1994; Henderson, 1998; Martin et al., 2010). This was consistent with our results showing the mean distribution location in deeper water compared to plaice and sole. This behaviour might help reduce interspecific competition. The bathymetry on the French side of the eastern English Channel dropped off steeply past 20 m deep, except for the Seine and Somme estuaries. Hence, optimal habitat (suitable and free of competition) for dab may be limited in other locations on the French coast as other flatfish occupied the coastal fringe.

The juveniles of plaice had a wide distribution along the southern coastline, up to the Seine estuary's mouth, and two clusters could be drawn from the centres of gravity. These clusters could also be seen highlighted on the first MAF (Figure A2). The G0 juveniles of plaice tend to distribute and feed in intertidal areas (Beyst et al., 2002). Coastal influence is central to their distribution, as described by Duval (1982). Clusters identified in our analysis may distinguish years when the Seine had a larger influence on their distribution potentially linked with the

river flow and benthic productivity. The "Banc du Ratier" is a pile of rocks and rubbles that was landscaped as a small artificial island during Le Havre harbour development of Le Havre in 2002–2005; it created new intertidal beaches potentially favourable to plaice settlement. Autumn, when sampling took place, corresponds to the migration of juvenile plaice from the intertidal area to deeper waters of around 5 m depth, increasing their catchability (Gibson et al. 2002, 2011). Although the intertidal area was not surveyed and the use of this part of the nursery was not be evaluated, we believe that our sampling scheme provided a fair representation of the distribution of juvenile plaice.

Sole is the species for which literature on nurseries was the most abundant, whether in the Seine (Rochette et al., 2010; Archambault et al., 2018), in the Channel (Eastwood et al., 2003) or on the French coast (Le Pape et al., 2003; Nicolas et al., 2007; Kostecki et al., 2010). Juveniles of sole were constantly found at the Seine estuary. However, the very low LIC index indicates that high densities were rarely seen at the same location, showing a high local heterogeneity in their distribution patterns. Depth and temperature affected the juvenile sole's distribution which is true for the juveniles of most flatfishes (Eastwood et al., 2003). However, some literature shows that river flow and salinity affected sole more than dab or plaice, perhaps because these factors have been studied more often with sole (Le Pape et al., 2003; Kostecki et al., 2010). River input brings essential nutrients to the ecosystem that enter the trophic chain and affect food availability for the juveniles. As it has been seen in other estuaries, sole tolerates a wider range of salinity (Power et al., 2000) compared to plaice and dab. Sole could then access resources not exploited by the two other species.

4.3. Temporal variation of spatial pattern

Juveniles' abundance was linked to habitat availability for their development (Parsons et al., 2014). Low densities may be the source of highly variable patterns. When abundance was low, it was expected that the pattern might vary from year to year as the habitable area is proportionally large. Hotspots of density were then expected to occur at different locations over the years and within the nursery area. Following

Dab

Plaice

Sole
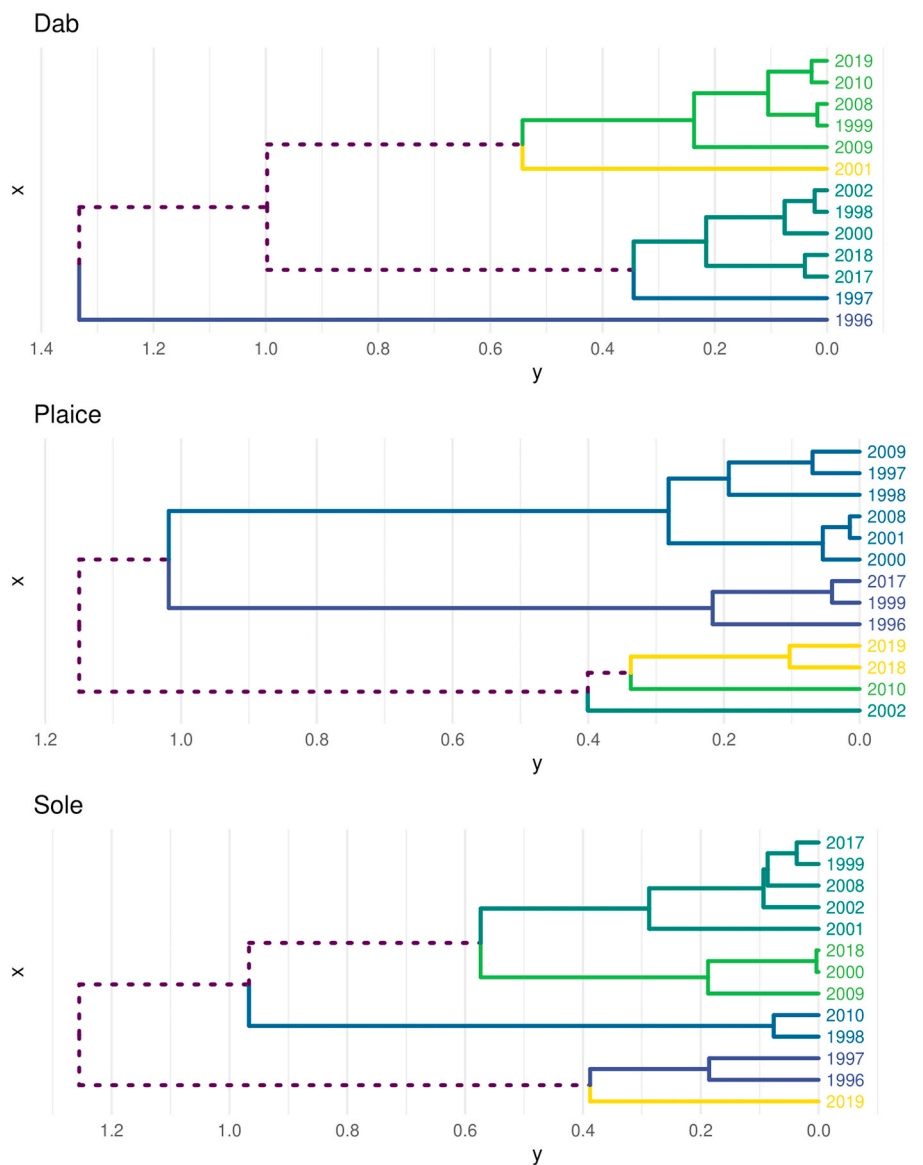
Fig. 6. Dendrograms built using Ward's criteria for each species based on scores of the first three MAF and displaying the number of groups indicated on simple structure index. The coloured set of branches indicates the clustering results for each species (a clustering is performed for each species, so cluster 4 of one species is not the same as cluster 4 of the other two species). Dashed lines are branches not related to a single cluster.

the decrease in flatfish abundance by harbour development in the area (Rochette et al., 2010), spatial patterns were expected to be highly variable (Figure A.3). Changes in the benthic communities in the Seine estuary were observed before and after the harbour development (Dauvin et al., 2010; Dauvin and Pezy, 2013). However, our results did not point to harbour development being the source of major changes in juveniles repartition in the nursery area. Instead, mean spatial distributions were stable despite known and extensive degradation (Le Pape et al., 2007). Two hypotheses could explain our results. First, it could be that there is no room for heterogeneity. Spatial patterns were restricted because the area available to settlement within the nursery has been reduced and biotic pressures were exerted by the co-occurrence of other flatfish species at the same time. These pressures constrained the distribution patterns of each population and the temporal variability observed. Second, the geostatistical methods used in this study did not directly take into consideration the raw densities but their standardised version, i.e. densities relative to their standard deviation. This method may have hidden larger differences in patterns before and after the harbour development. The state of juvenile flatfish in the Seine estuary

was impacted by anthropogenic disturbances, as observed by Gilliers et al. (2006). One clear example is the trend in juveniles' density (See figure A.3). Although the dataset seems to show changes in abundance, the dynamic described in spatial patterns did not correlate with the disturbances. Hence, a distinction can be made between the population's response in spatial distributions and demography to disturbances. However, the standardisation was necessary due to the variance in the data. The low densities induced a high variability on spatial patterns that may have masked an anthropogenic signal. These low densities coupled with the high heterogeneity of benthic assemblage at the mouth of the estuary (Ghertsos et al., 2001) may explain the high variability in juveniles' distribution.

Some singletons detected by the MAF clustering could however be explained by particular hydrodynamic conditions. River flow is an environmental driver often essential in flatfish nursery as it controls habitat availability through salinity (Bos and Thiel, 2006) or benthic production (Le Pape et al., 2003). As pointed out in Dauvin and Pezy (2013), 2001 was the year with the maximum mean flow for the period of 1990–2012. This was highlighted in the dab clusterings where 2001 is

one of the singletons on the MAF dendrogram and on the GIC network being only connected to 2008 by one edge. This potentially reflected a higher influence of freshwater input on this species distribution than on sole or plaice.

Seasonal movements cannot be evaluated in the current study because of the yearly survey. However, Brind'Amour et al. (2018) previously identified that all three species' juveniles displayed an identical seasonal migration pattern, moving out of the estuary in summer and coming back in autumn. If all three species globally had the same movement, it is possible that segregation, as it was observed here in autumn, may be constant in time.

4.4. Conclusion and perspectives

The investigation of spatial patterns in the nursery showed that even though relatively small areas are used for a single species, the whole space considered as a nursery was used due to ecological constraints. Segregation in the spatial distribution was recurrent, but spatial patterns themselves are unstable, partly because of the nursery degradation. Further studies should emphasise the characteristics of the eastern Bay of the Seine ecosystem to understand how environmental variables can affect the spatial distribution of communities during the juvenile phase. Putting together the spatial knowledge of this study and abiotic parameters will give a better understanding of species/environment relationship in a disturbed nursery (Peterson, 2003). The use of spatial indices has been reviewed and encouraged in Rufino et al. (2018) to create the most efficient management for a given species. These management methods need to integrate as much as possible the ecological knowledge to maximise survival during the juvenile phase that is crucial to exploited populations.

CRediT authorship contribution statement

Thibault Cariou: Formal analysis, Investigation, Data curation, Writing – original draft, Visualization. **Laurent Dubroca:** Conceptualization, Investigation, Writing – original draft, Supervision. **Camille Vogel:** Conceptualization, Investigation, Writing – original draft, Supervision, Project administration, Funding acquisition. **Nicolas Bez:** Conceptualization, Investigation, Writing – original draft, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2021.107471.

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