Relationship between interannual variations of the river plume and the extent of nursery grounds for the common sole (*Solea solea*, L.) in Vilaine Bay. Effects on recruitment variability

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**Abstract**

This study describes the spatial distribution of juvenile sole on the basis of a 10-year beam trawl survey of Vilaine Bay, an estuarine nursery ground within the Bay of Biscay (France). A significant relationship between fluvial discharges in winter-spring and the area covered by high densities of 0-group juveniles was indicative of the favourable effects of freshwater supply on nursery size. The extent of the river plume influences both the larval supply and the size and biotic capacity of habitats in estuarine nursery grounds and determines the number of juveniles produced. The correlation between river flow and sole recruitment for Vilaine Bay was confirmed for the Bay of Biscay stock. As the recruitment of the Bay of Biscay sole stock depends partly on the influence of river plumes on nursery grounds, it appears to be less variable than for other sole stocks affected essentially by larval supply. The balance between the different factors influencing recruitment differs according to the area concerned, and recruitment variability depends on the respective roles of these factors.

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**Keywords:** Fluvial discharge; *Solea solea*; Estuarine nursery ground; Recruitment variability

1. **Introduction**

As their nursery grounds are mainly located in estuarine and coastal areas (Lenanton and Potter, 1987), various marine fish species widely distributed on the continental shelf are directly affected by freshwater inputs. Survival and growth of early stages are maximal in estuarine habitats, which makes these species estuarine-dependent (Miller et al., 1984). Quantitative (nursery area) and qualitative factors (food supply, temperature, mortality due to predation, etc.) have a considerable influence on recruitment level (overviews in Gibson, 1994; Van der Veer et al., 2000) and the relation between recruitment level and the area of estuarine nursery grounds has been demonstrated in comparisons of different systems (Rijnsdorp et al., 1992). On the other hand, the role played by land-based run-off in increasing coastal fishery production has been recognised in many places and especially for the sole (Salen-Picard et al., 2002). The present study investigated whether interannual variation in the extent of a river plume affects the estuarine nursery grounds and consequently the recruitment level.
The relation between the interannual variability of river flow and young of the year (YoY) sole distribution was studied in Vilaine Bay, an estuarine nursery ground within the Bay of Biscay. The processes relating fluvial discharge to the distribution and density of 0-group sole were investigated, and the results were analysed with respect to the determinism of flatfish recruitment. The relationship between recruitment determinism and variability was then considered.

2. Material and methods

2.1. Study area

The Bay of Biscay is an arm of the North Atlantic indenting the west coast of France (ICES Area VIIIa/b, Anon., 2003; Fig. 1) where sole is the most frequent and abundant fish (Koutsikopoulos et al., 1995) and the most heavily exploited large demersal species [5000 tons/year, Anon., 2003, for a value of 50 10^6 tons/year].

Fig. 1. Map of Vilaine Bay showing sediment types, 5, 10, 20 and 30 m isobaths, the full study site (indicated by black arrows), and the reduced study site (indicated by black frame). Inset lower left corner: the location of Vilaine Bay in France.
The Bay of Biscay is regarded as a unit for stock management of the common sole year (Anon., 2003). Vilaine Bay (Fig. 1), a shallow coastal inlet of the northern Bay of Biscay, opens out from the mouth of a silting-up estuary. The bottom is covered with soft fine sand and mud (Pinot and Vaney, 1972; Fig. 1). This body of water is an important nursery grounds for sole within the Bay of Biscay (Koutsikopoulos et al., 1989a).

2.2. Beam trawl surveys in Vilaine Bay

Thirteen surveys were conducted in Vilaine Bay in September from 1985 to 2002 (IFREMER, RV ‘Gwen Drez’, Table 1). Juvenile flatfish are still in their growth period in September, making this the most suitable time for the study of nursery grounds: the distribution of juvenile sole is then representative of the productive period (Dorel et al., 1991). Moreover, the problems of selectivity and size-dependent catchability, very important in early summer, are limited at the end of the growth period. The beam trawl used in the surveys had an opening 2.9 m wide and 0.50 m high, and the codend of the net had 20-mm stretched mesh. The trawl had no tickler chain ahead of the foot rope. Operating conditions were checked and standardised from the first survey. Hauls were made only in daylight at neap tides at 2.5 knots for 20 min (each covering 4500 m² on average).

2.3. Distribution of 0 group sole in Vilaine Bay

All sole were counted and measured. The age groups were established after otolith reading for each year of the investigation. As susceptibility to environmental changes (such as temperature, oxygen, food) is high for the youngest juvenile sole and then decreases with age (Koutsikopoulos et al., 1989b), the relation between juvenile distribution and river flow was studied for 0-group sole selected from this age determination.

Sampling schemes need to be very similar from one year to another for meaningful comparison of 0-group sole distributions on the basis of trawling data. As the upstream and downstream limits differed for the surveys, it was necessary to select the lowest area common to all ten surveys. Thus, the limits of this reduced area were set at 47.375° N on the south, 47.513° N on the north, 2.658° W on the west and 2.513° W on the east (Fig. 1). Trawl hauls performed outside this area were excluded from the analyses. This study area is the part of Vilaine Bay that stretches from the river mouth to about 10 m depth (Fig. 1). Here, the number of trawl hauls per survey varied from 18 to 43 (Table 1) but their distribution was comparable from one year to another (Fig. 2) and the sampling scheme was deemed similar enough for all surveys to allow comparisons of juvenile sole distribution and density.

0-group sole densities were calculated for each trawl haul (number of 0-group sole per km²) and the average and the standard deviations of this density per yearly survey were first calculated. Then, a standardised extrapolation method was used to generate the annual maps of 0-group sole distribution; this method involves the following steps:

- 0-group sole densities per trawl haul were log-transformed with a \( y = \ln(x + 1) \) transformation in order to take 0 values into account.

- Trawling stations were established at discrete, irregularly spaced sites. The ‘Spatial Analyst’ extension of ‘Arcview GIS’ software (ESRI, Inc) was used to convert these data into continuous regularly spaced annual grids by means of inverse distance weighting. For each survey year, an interpolated grid was generated from log-transformed 0-group sole densities. This grid used four significant neighbours and a weighting power of two. Overlay analysis was simplified by

<table>
<thead>
<tr>
<th>Year</th>
<th>River flow (L s⁻¹)</th>
<th>Number of trawl hauls in the study area</th>
<th>Average density (fish km⁻²)</th>
<th>Standard error of the density (fish km⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1985</td>
<td>129540</td>
<td>39</td>
<td>3996</td>
<td>109763</td>
</tr>
<tr>
<td>1986</td>
<td>120460</td>
<td>39</td>
<td>822</td>
<td>17084</td>
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<tr>
<td>1987</td>
<td>73560</td>
<td>41</td>
<td>614</td>
<td>18016</td>
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<tr>
<td>1988</td>
<td>229000</td>
<td>40</td>
<td>8584</td>
<td>130538</td>
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<td>1989</td>
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<td>43</td>
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<td>147986</td>
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<td>1990</td>
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<td>1997</td>
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<td>59403</td>
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<tr>
<td>2002</td>
<td>18</td>
<td>18</td>
<td>1991</td>
<td>49097</td>
</tr>
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</table>
maintaining uniformity among the annual 227 lines and 239 columns in the specified area. As the surface covered by land in the study area was negligible, no barriers, additional zero values or boundary conditions were used in this interpolation.

– All of the 445 trawl hauls performed during the 13 surveys in the study area were taken into account in computing the density for the median of the positive values and the value for which 75% of the positive densities were lower (designated as N75). Each annual interpolated grid was then used to generate three isolines marking the limits between null and positive densities and between densities below and above the median and the N75 value. Thus, for each year of the survey, four density classes are indicated on the interpolated maps: 0, [0,median], [median,N75], >N75.

– The respective areas covered by the four density classes were computed with ‘Spatial Analyst’ software. Three values were taken into account in determining the extent of the nursery grounds: the area in which there were no 0-group sole, the area covered by densities higher than the median value (sum of the two classes [median, N75]) and >N75), and the area covered by densities higher than the N75 value.

2.4. Relation between juvenile distribution and river flow

Data for monthly flows of the Vilaine River were obtained from the national hydrologic databank of the French Ministry of the Environment from 1985 to 2001, these data not being available for 2002. A typology of the interannual and seasonal variations of this flow was used in a previous work (Le Pape et al., in press) to select the period most likely to affect 0-group sole distribution:

– This period appears to be at the beginning of their benthic life, from April to June (Marchand, 1991; Amara et al., 2000), when the juvenile sole are especially dependent on habitat quality (Koutsikopoulos et al., 1989a).

– Moreover, as a period of rising flow (October to May) has a greater influence than a low-water period, the distribution of juvenile sole needs to be considered...
with respect to river flow conditions. According to Puillat et al. (in press), a five-month period is appropriate for studying the effects of river flow conditions on the hydrodynamic situation in the Bay of Biscay.

Thus, the density and the distribution of 0-group sole during the summer growth period (as observed in September) was considered in relation to Vilaine river flow from January to May. The first part of the Vilaine river rising period was regarded as too early, in terms of sole settlement period to influence juvenile distribution and the low-water period, when freshwater input into Vilaine Bay is very limited, begins in June.

Annual average densities on the study area, annual maps of interpolated data for the distribution of 0-group sole and the areas covered by the different density classes were compared to this river flow from 1985 to 2001.

2.5. Variability of the recruitment in the Bay of Biscay

Abundance of 1-group sole was estimated from VPA analysis from 1984 to 1999 in the ICES division VIIIa/b. (Anon., 2003). The uncertainty of this analytical technique for estimating population size for the more recent years prevents VPA outputs being taken into account for those years. These data allowed us to compute a standardised coefficient of variability (Rijnsdorp et al., 1992): As recruitment series generally have a log-normal distribution, variations [expressed as standard deviations (SD)] were calculated from loge-transformed data. The antilog of the standard deviation, $e^{SD}$, which gives the variance as a multiplicative factor, was converted into a coefficient of variability (CV in %): $CV = (e^{SD} - 1) \times 100$. It was then possible to compare sole recruitment variability for the Bay of Biscay with that of other sole stocks studied by Rijnsdorp et al. (1992), who used the same method for the same age group.

3. Results

Interpolated maps of 0-group sole in Vilaine Bay (Fig. 2) showed a main concentration near the river mouth. The densities generally followed a decreasing gradient from the river mouth to the downstream limit of the study area, where they are very generally null or lower than the median value. Thus, these maps indicated that the study area was large enough to determine the extent of the 0-group in Vilaine Bay.

Fig. 2 indicates the interannual variability of juvenile distribution. The areas covered by high densities differed from one year to another and become larger toward the open sea with increased river flow. Linear regression analysis showed a significant positive relation between winter-spring flow (January to May) and the areas covered by 0-group densities higher than the median value ($\rho = 0.81, \alpha < 10^{-3}$) and the N75 value ($\rho = 0.81, \alpha < 10^{-3}$). Conversely, the proportion of the area covered by null densities, mainly located at the downstream limit of the study area (Fig. 2), decreased significantly with river flow ($\rho = -0.68, \alpha < 10^{-2}$). However, the estimation of 0 group sole density was vitiated by a considerable standard error.

Fig. 3. Scatter plot of the relation between winter-spring flows and a) the zone involving higher than median densities of 0-group sole. b) the estimated density of 0-group sole. (Years are indicated on the plots).
(Table 1), the coefficient of variation reaching 24 on average in the 13 surveys. Nevertheless, the average density of 0 group sole in the study area was positively correlated to the Vilaine flow (Fig. 3b, $\rho = 0.7$, $\alpha < 10^{-5}$).

These results indicate that fluvial discharges during the first five months of the year (the flow period before or at the beginning of larval settlement) had a positive influence on the extent of the nursery grounds. As the area covered by high densities of 0-group sole increased with river flow, the number of juveniles located in Vilaine Bay also increased. This implies a significant positive relationship between fluvial discharges in winter-spring and densities of 0-group juveniles in Vilaine Bay. These results seemed to explain the general trend observed in sole density in three successive periods (Table 1): a period of high recruitment in the 1980s, with mainly wet years, then a period of low recruitment in the 1990s, with mainly dry years, followed by two high recruitment years (2000 and 2001) when the river flow increased again. Unfortunately, data on the river flow were not available for 2002.

From 1984 to 1999, the population of 1-group sole, estimated with VPA analysis (Anon., 2003), ranged from 24053 to 42325 $10^6$ individuals and the coefficient of variability calculated for sole recruitment in the Bay of Biscay was 22%. This coefficient was 97 (Irish Sea) to 130% (North Sea) for the most variable stocks and from 34 to 55% for three stocks located between Bristol Bay and the Eastern Channel (Rijnsdorp et al., 1992). Therefore, sole recruitment appears as very constant in the Bay of Biscay.

4. Discussion

4.1. Influence of river flow on the extent of the nursery grounds

The variability of river flow affects both the extent of coastal nursery grounds in the Vilaine Bay and the number of juvenile sole. This relation was moreover confirmed from quantitative estimates of the global number of juvenile sole surviving into the second autumn of their existence (Le Pape et al., in press). According to Boehlert and Mundy (1988), interannual variations of winter-spring river flows can affect the coastal habitat, and hence recruitment strength, directly and indirectly:

Direct effect: the offshore range of the low-salinity plume. In the region subject to Vilaine river flows, as far as 30 to 40 km from the estuary, the water layer near the bottom moves towards the coast in conjunction with offshore surface movements (Lazure and Salomon, 1991), facilitating the transport of transforming larvae towards the nursery area (Koutsikopoulos et al., 1991). Hence, a considerable winter-spring river flow favours the immigration of young stages and tends to maximise the number of 0-group fish in the nursery. Density-dependent habitat selection processes can lead to an expansion of population range to marginal habitats towards the open sea during wet years, when abundance is high (McCall, 1990).

Indirect effect: the quality of the invertebrate benthic community that constitutes the food supply for young fish on nursery grounds (Howell et al., 1999; McConnaughey and Smith, 2000; Phelan et al., 2001). For the Vilaine and Loire (an adjacent river) estuaries, Marchand and Masson (1989) and Marchand (1993) have shown the impact of salinity and turbidity on the settling of the benthic communities (dominated by young stages of polychaetes and bivalves) preyed upon by euryhaline fishes and especially the common sole. The development of a community tolerant to low salinity provides suitable food for young sole (Costa and Bruxelas, 1989), which can rely on this nearly limitless supply (Amara et al., 2001) until at least the second autumn of their life (Dorel et al., 1991). In the same manner, Darnaude et al. (in prep.) conclude that high land-based run-off is favourable for the productivity of invertebrate prey, and hence for the productivity of the common sole and other flatfish species in the Mediterranean. This relation between food availability and juvenile abundance was also confirmed by Riou et al. (2001) from the spatial link between the more productive sectors and the nursery grounds of the sole stock of the Eastern Channel.

Numerous processes occur in between the settling of larvae and the end of the productive period in autumn, and the present study does not allow us to distinguish the respective influences of these two mechanisms. Nevertheless, interannual variability of larval abundance (Koutsikopoulos and Lacroix, 1992) is lower than that of juveniles in Vilaine Bay (Dorel et
al., 1991; Le Pape et al., in press and the present study) and does not seem to be large enough to explain the fluctuations of juvenile abundance. Hence, the influence of river flow seems to come from its impact on habitat size rather than from its role in the hydrodynamic transport of larvae.

The positive effect of estuarine influence on sole recruitment depends on sufficient river flow. Human pressure is especially high in estuarine areas and their watersheds. Eutrophication, related to nutrient excess, and/or pollution loading could affect both benthic prey (Ferber, 2001) and the growth and the survival of juvenile fish (Meng et al., 2000) in estuarine nursery grounds. In Vilaine Bay, freshwater inputs are very limited during the productive period (Le Pape et al., in press). Nevertheless, the Vilaine river is an important source of nutrients and eutrophication events occur in the Bay, particularly in summer (Chapelle et al., 1994). In July 1982, an anoxic crisis led to the death of various organisms (Rossignol-Strick, 1985) and delayed growth of 0-group sole (Koutsikopoulos et al., 1989b). The positive influence of the river flow on larval supply and nursery habitat can be damped by such anthropogenic disturbances.

4.2. General interest for determination of recruitment variability

The fluvial regime determines the nursery area, thereby affecting sole recruitment at a local scale in the Vilaine Bay. This relation was moreover confirmed at the scale of the French part of the Bay of Biscay from the relation between freshwater inputs in winter-spring during the year of birth and the density of juveniles in the open sea in spring during their third year of existence (Le Pape et al., in press). In this work, survey data were used rather than the Virtual Population Analysis output to avoid any bias due to the analytical technique applied to estimate population size. Nevertheless, the high recruitment period of the 1980s, a mainly wet period, followed by low recruitment during the 1990s, a drier period, is also confirmed by VPA outputs at the stock scale (ICES division VIIIa/b; Anon., 2003). Unfortunately, it is not possible to follow this comparison for the more recent years, because reliable VPA outputs are not yet available. Hence, in the Bay of Biscay, river flow would seem to be an important factor governing the abundance of young sole. A similar positive effect of river flow during the flood regime peak on recruitment has already been demonstrated for exploited fish communities (Mérona and Gascuel, 1993; Quiñones and Montes, 2001) and in particular for the common sole in the Mediterranean (Salen-Picard et al., 2002).

A number of factors (overview in Van der Veer et al., 2000), including hydrodynamics during pelagic larval life (Nielsen et al., 1998; Chant et al., 2000), density-dependent effects on food supply and predation (Cowan et al., 2000), and the size of the juvenile habitat (Schmitt and Holbrook, 2000, and the present study), can influence the recruitment success of fish, and especially flatfish. The balance among these factors differs according to area. Flatfish populations can exhibit different strategies, and the mechanisms determining year-class strength are not always the same (Nash and Geffen, 2000).

Rijnsdorp et al., (1992) indicated a higher variability from survey estimates than for VPA series and the present study verified this conclusion. Nevertheless, the variability estimated from trawling surveys varies significantly with the scale of study and is moreover not well estimated because of the large standard error associated to the density. It is not realistic to compare recruitment variability from different surveys using various spatial sampling protocols. On the contrary, such a comparison can be realised from VPA estimates realised at a stock scale (Rijnsdorp et al., 1992), the uncertainty of VPA outputs after several years of convergence being limited with regards to survey data. As demonstrated by Forest (1995) and confirmed by the present study, the variation in the recruitment rate for Bay of Biscay sole stock is very slight compared to that for other sole stocks and stocks of other species. The determination of sole recruitment in the Bay of Biscay allows an explanation of this slight variability: variability-generating processes occur during all life-stages of flatfish, but only those operating at the 3-D pelagic egg and larval stages can be of major importance (Van der Veer et al., 2000). In the Bay of Biscay, sole recruitment is at least partly regulated after settlement and transfer to the 2-D environment. The variability is reduced in comparison with other stocks in which the determination of the pelagic phase is stronger, e.g. in the North Sea (Rijnsdorp et al., 1992) and the Irish Sea (Symonds and Rogers, 1995). As described in the concentration
hypothesis by Iles and Beverton (2000), variability is least in those stocks that possess a high degree of compensation caused by damping density-dependent effects related to nursery habitat capacity. These authors illustrate this theory with flatfish species and especially sole. The present study seems to demonstrate that this conclusion is especially true for the Bay of Biscay stock.

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