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The transport of anchovy larvae and juveniles across the Bay of Biscay studied using otolith increments and a 3D hydrodynamic model

by

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Anchovy *Engraulis encrasicolus* concentrates in the SE corner of the Bay of Biscay during the spawning season from May to July, especially in the plumes of the French rivers Gironde and Adour. In autumn, juveniles are found dispersed in many different habitats, off the French and Spanish coasts, outside the shelf break and in a larger box than the SE corner of the Bay. A 3D hydrodynamic model capable of reliably simulating the flow field in the surface layers was developed by IFREMER. It was used as a first fisheries application to simulate the transport processes affecting Biscay anchovy from the egg to the juvenile stages in 1999. Juveniles were collected in different sites during a survey in September 1999. Their birth-dates were estimated by interpreting the otolith increments. Virtual buoys were released on the grid of the hydrodynamic model at the birth-dates and their trajectories were tracked. The buoys that were found close to the juvenile sampling sites at the appropriate dates were selected as potential transport trajectories experienced by the larvae and juveniles during their development. The probabilities of transport from the spawning to the potential nursery grounds were estimated. A simplified spawning model was used to simulate the transport pattern and the probable distribution of juveniles at the population scale. The simulation shows a general transport to the south-west across the Bay of Biscay. SE Biscay appears as a retention area mainly seeded by the spawning grounds located over the French shelf. An advective system to the west would spread along the Spanish shelf. The distribution of anchovy juveniles predicted by the model is coherent with the September 1999 survey. The transport model was forced by the climatic conditions in 1999. The wind regime in 1999 was close to the average regime from 1986 to 2000. Therefore this transport model would be representative of the general transport scheme of anchovy larvae and juveniles in the Bay of Biscay.

Keywords : transport, larva, Anchovy, Biscay, otolith, recruitment

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INTRODUCTION

Transport processes are thought to be a main determinant in the recruitment of marine fishes through their interaction with mortality processes from the egg to the juvenile stages. In the Bay of Biscay transport from the spawning to the nursery grounds is poorly known. Anchovy *Engraulis encrasicolus* concentrates in the SE corner of the Bay during the spawning season from May to July. Although spawning occurs in different areas (i.e., shelf, river plumes, shelf break, open ocean outside the shelf), the major spawning grounds in the past decade have been the plumes of the French rivers Gironde and Adour. In autumn, juveniles are found dispersed in many different habitats, off the French and Spanish coasts, outside the shelf break and in a larger box than the SE corner of the Bay.

What are the spatio-temporal climatic connections between the nursery and the spawning sites? Where are exported the anchovy larvae born on the major spawning grounds of Gironde and Adour? In particular, can anchovy larvae born on these spawning grounds be exported to the nursery grounds off the Spanish coast? To answer such questions, it is necessary to use a hydrodynamic model capable of reliably simulating the flow field in the surface layers on the shelf but also outside the shelf. Such model was developed by IFREMER and this is a first fisheries application.

Juveniles were collected in different sites during a survey in September 1999. Their birth-dates were estimated by interpreting the otolith increments. Virtual buoys were released on the grid of the hydrodynamic model at the birth-dates and their trajectories were tracked. The buoys that were found close to the juvenile sampling sites at the appropriate dates were selected as potential transport trajectories experienced by the larvae and juveniles during their development. The probablities of transport from the spawning to the sampling sites were estimated. These spatial probabilities were used to investigate the transport processes affecting anchovy from the egg to the juvenile stages. A simplified seasonal model was set in order to reproduce the spatio-temporal pattern of spawning at the population scale.

The probable distribution of the juveniles predicted by the transport model is compared with the September 1999 survey. The transport scheme simulated for 1999 and its connection to the wind regime are analysed. The generalisation of this transport pattern to other years is then discussed using the wind data from 1986 to 2000.

MATERIALS AND METHODS

Determination of birth dates using otolith microstructure analysis

In September 1999, an ichtyoplankton survey (Juvesu survey conducted by IFREMER and AZTI) was performed in SE Biscay, off the Spanish coast and on the continental shelf off the Gironde mouth, which are known as potential nursery grounds for juvenile anchovy *Engraulis encrasicolus*. Juveniles were sampled at sea surface (0-20 m) with hauls at 3-4 knots of a pelagic trawl mounted with a 4 cm mesh over the codend. 17 hauls were performed (cf. Fig. 1) : 12 off the Spanish coast and 5 on the French continental shelf. 39 juveniles sampled off the Spanish coast and 49 juveniles sampled on the French continental shelf were analysed.

The age of each juvenile was counted in daily increments from the mark of mouth opening (Campana and Jones, 1992). Subsequently we will use "hatch date" or "date of mouth opening" equally. The date of hatch was then deduced from the age estimated and the date of sampling.

Tracking of water masses trajectories in a 3D hydrodynamic model

A 3D model of the Bay of Biscay (Jégou *et al*., in press) shelf has been developed at IFREMER to study the hydrodynamics and the evolution of hydrology. This model simulates the evolution of currents, temperature and salinity induced by the main dynamic processes: tides, wind-induced circulation and thermohaline circulation. The latter is generated by temperature and salinity gradients induced by the heat budget at the surface and discharges of the rivers Loire, Gironde and Adour.

The simulation domain corresponds to the whole Bay of Biscay, as an expansion of the former French continental shelf model (Jégou and Lazure, 1995; Lazure et Jégou, 1998). It extends from the French and Spanish coasts to the abyssal deep to the south of the English Channel entrance (49°N) and to the east of the 8°W meridian. The numerical grid has a 5 km x 5 km mesh on the horizontal plane and 30 levels on the vertical. The time step is approximately 900 seconds corresponding to a fixed portion of the tidal cycle. The open boundary conditions (sea level elevation and currents) are produced by a larger 2D barotropic model extending from Portugal to Iceland which is forced by the semi-diurnal tide and by wind fields. Winds measured every 3 hours by Météo-France are used as a surface condition and a radiation condition is used for sea water temperature. Daily run-off of the Loire, Gironde and Adour rivers are used as boundary conditions. The temperature and salinity fields calculated by the model have been validated by comparison with survey data and with satellite observations (Jégou *et al*., in press). The model is not able to reproduce all the local retention mechanisms, especially in the very coastal areas.

Anchovy larvae and juveniles are found in the surface layer (0-30 m) mainly above the thermocline, where they carry out daily vertical migrations (Palomera, 1991, Garcia *et al*., 1998). Therefore we considered the upper 30 m layer as representative of the habitat of anchovy larvae and juveniles. We defined a water mass as the upper 30 m water column at a given location. Each water mass was tracked in the hydrodynamic model by a virtual buoy sensitive to average currents in the 30 m surface layer.

Virtual buoys marking unit water masses were released (cf. Fig. 1) from a 10 km x 10 km grid south of 47° N every week during the hatching period of the sampled juveniles (i.e. May to July). The buoys trajectories were stopped on the sampling dates (mid-September). Then we considered two types of virtual buoy trajectories : i) those conditioned by their arrival location in the sampling areas of the juvenile survey in September 1999 and ii) those conditioned by their starting location in the spawning grounds evidenced by egg surveys.

Origin of the juveniles sampled in September

The trajectories beginning on the hatch period of a given sample of juveniles and ending in their sampling area on sampling dates were first selected. They represent the trajectories potentially experienced by the juveniles during their early life. Individuals from the egg to the juvenile stages are considered to be transported passively by the average currents in the 30 m surface layer. The starting locations of the selected trajectories correspond to the potential hatching area of the juveniles. The arrival box corresponding to a given sample of juveniles was defined as the 21 x 21 nautical miles (approx. 0.5 ° in longitude) square centered on the mean position of the related trawling.

Transport of larvae from the spawning grounds

The trajectories starting from the known spawning areas during May, June and July and ending on 14 September (last date of sampling and end of the simulation) were also selected.

Six different spawning strata (Fig. 2) were defined using the egg distribution pattern observed in 1999 (BIOMAN survey conducted by AZTI) and in previous years (cf. Motos *et al*., 1996). The "Gironde East" and "Adour" strata correspond to the major and most regular spawning grounds. The "Landes" (between the former) and "Gironde West" strata are regular spawning grounds over the shelf and the continental slope. The "Vendée" and "North Spain" strata are supposed to be more marginal or less regular spawning locations.

The Bay of Biscay was divided into a grid of squares, each 21 x 21 nautical miles in size. We then calculated the probability of transport from each spawning stratum and each week (release of the buoys) to each square of the grid on 14 September (arrival of the buoys). The probability of transport from a given spawning stratum to a given square of the grid is the ratio of the number of buoys that arrived in the square relative to the total number of buoys released in the spawning stratum. These probabilities were used to map the probable distribution on mid-September of the juveniles stemming from May, June and July spawnings in each stratum.

Spawning model and subsequent juvenile distribution

The spatial probabilities were used to simulate the seasonal process of production and transport of larvae at the population scale. To account for the spatial distribution of anchovy spawning, the probabilities related to the different spawning areas were given coefficients proportional to their relative abundance in eggs : Vendée, Gironde West, Gironde East, Landes, Adour and North Spain areas were given the respective weights 1, 2, 3, 2, 3, 1. To simulate the temporal evolution of anchovy spawning, the probabilities related to May, June and July were given a monthly coefficient (2,3 and 1 respectively). The probable spatial distribution of the juveniles on mid-September was then calculated by summing for each square of the grid the probabilities of transport weighted by their spatial and temporal coefficients.

RESULTS AND DISCUSSION

Spatial and temporal origin of the juveniles

The sampled anchovy juveniles were 54 to 128 days old (after hatching) and hatched from 10 May to 16 July 1999. The hatch dates of the juveniles from each sample (cf. Fig.3) show a peak between 20 June and 10 July (Julian days 170 and 190). The hatch dates of the juveniles from all samples show a peak at the end of June (around Julian day 175). This peak may i) represent the main "survival window" of the season or/and ii) be linked to the selectivity of the trawl or less probably iii) be due to a spatio-temporal match between this micro-cohort and the survey.

The areas where the different samples of juveniles were caught in September 1999 and the possible locations of their hatching (spawning) origin are shown on Figure 4. The juveniles sampled near the shelf break off Gironde (samples 13 and 14 of Fig.1) supposedly originated from areas over the French continental shelf north of 45.5°N. The juveniles sampled off the Spanish coast east of 3°W (samples 9 and 10) supposedly originated from spawning areas over the French continental shelf between the latitudes of Gironde and Adour. The juveniles sampled off the Spanish coast west of 3°W (sample 6) supposedly originated from areas over and off the French continental slope south of 45 °N.

These first simulations show a general transport to the south-west across the Bay of Biscay from the French shelf spawning grounds towards nursery grounds over and off the Spanish and French shelf breaks.

Transport of larvae from the spawning grounds

Figure 5 shows the mid-September location of the virtual buoys that were released in each spawning area on the last week of June, when most of the sampled juveniles were hatched (peak on Fig. 3). Figure 6, 7 and 8 show the spatial distribution of the probabilities of transport of the virtual buoys released in each spawning area and tracked until mid-September.

Three distinct transport patterns appear in relation to the different spawning strata :
1) The buoys from the Vendee and Gironde West areas remain on the French shelf and slope. Gironde West shows a high level of retention.
2) The buoys from the Gironde East and Landes areas show a moderate drift to the south-west and remain in the inner part of the Bay of Biscay. As a result, the trajectories from Gironde East spread in

the waters over the French shelf break. The trajectories from Landes end off the Spanish shelf break east of 6°W on mid-September.
3) The buoys from the Adour and North Spain areas show an important drift to the west and north-west. As a result, the trajectories from Adour spread over and off the Spanish shelf break. The trajectories from North Spain are advected to the outer and deeper part of the Bay.

The distributions of the virtual buoys related to May, June and July spawnings are rather similar. The progress of the drift with the "age" of the buoys is more obvious in the most advective systems (North Spain, Adour). The local retention mechanisms near the coast may be underestimated by the model. Only passive transport is considered.

Spawning model and subsequent juvenile distribution

Figure 9 shows the result of a simulation of the annual egg production and transport process at the population scale. The weighted probabilities of transport from the spawning grounds were summed over the season in order to reproduce the spatio-temporal pattern of spawning. The main nursery areas of juvenile anchovies predicted by this simulation would be the waters over and off the French and Spanish shelf breaks in south-east Biscay.

A direct comparison between the results of the simulation and the juvenile survey would not be valid. Only a limited part of the Bay was surveyed in September 1999 (cf. Fig. 1). Besides, the model only accounts for the transport processes and not for the mortality processes. In the model individuals from the egg to the juvenile stages are considered to be transported passively by the average currents in the 30 m surface layer.
Though the survey and the simulation agree on several points. The anchovy juveniles were found in the waters over and off the shelf breaks in agreement with the most probable nursery areas in the model. No juvenile was found in the coastal area near Gironde as predicted by the model. The oldest juveniles were found in the most retentive area according to the transport model, i.e. over the outer part of the French shelf west of Gironde. The less regular spawning grounds off North Spain also correspond to the most advective area in the model, characterised by a drift to the outer part of the Bay.

A synoptic description of the simulated transport scheme affecting Biscay anchovy from the egg to the juvenile stages in 1999 is illustrated on Figure 10. The south-eastern part of the Bay can be considered as a retention area for anchovy larvae originating from the main spawning grounds. An advection system to the west would spread along the Spanish shelf.

The wind forcing in 1999 and in the past 20 years

Winds are an indicator of the climatic regime and a main determinant of surface circulation in Biscay from May to September. The cumulative vector diagram of wind stress from May to September 1999 at Chassiron semaphore (Fig. 11) shows a dominant north-western wind regime. The simulated circulation to the south and south-west over and out of the French shelf corresponds to the Ekman drift forced by this dominant wind regime. The simulated drift to the west along the Spanish shelf break may appear as a flush out of the south-eastern part of the Bay resulting from this circulation.

The years from 1986 to 2000 were all characterised by a north-western wind regime from May to September according to Chassiron semaphore observations (cf. Fig. 11). The 1999 wind regime is not an extreme one (Fig. 12), the western component of the wind being slightly higher and the southern component being slightly lower than in the mean regime. Therefore the transport scheme simulated for 1999 can be considered as representative of the broad outline of the general transport scheme from May to September in the Bay of Biscay.

CONCLUSION

A 3D hydrodynamic model of the Bay of Biscay was used to simulate the transport processes affecting anchovy from the egg to the juvenile stages in 1999. Neither active transport nor mortality process was considered. The model shows a general transport to the south-west across the Bay of Biscay. SE Biscay appears as a retention area mainly seeded by the spawning grounds located over the French shelf. An advection system to the west would spread along the Spanish shelf. The distribution of anchovy juveniles over and off the shelf breaks in SE Biscay predicted by the model is coherent with a juvenile survey performed in September 1999. The transport scheme for 1999 would be representative of the general transport scheme from May to September in the Bay of Biscay.

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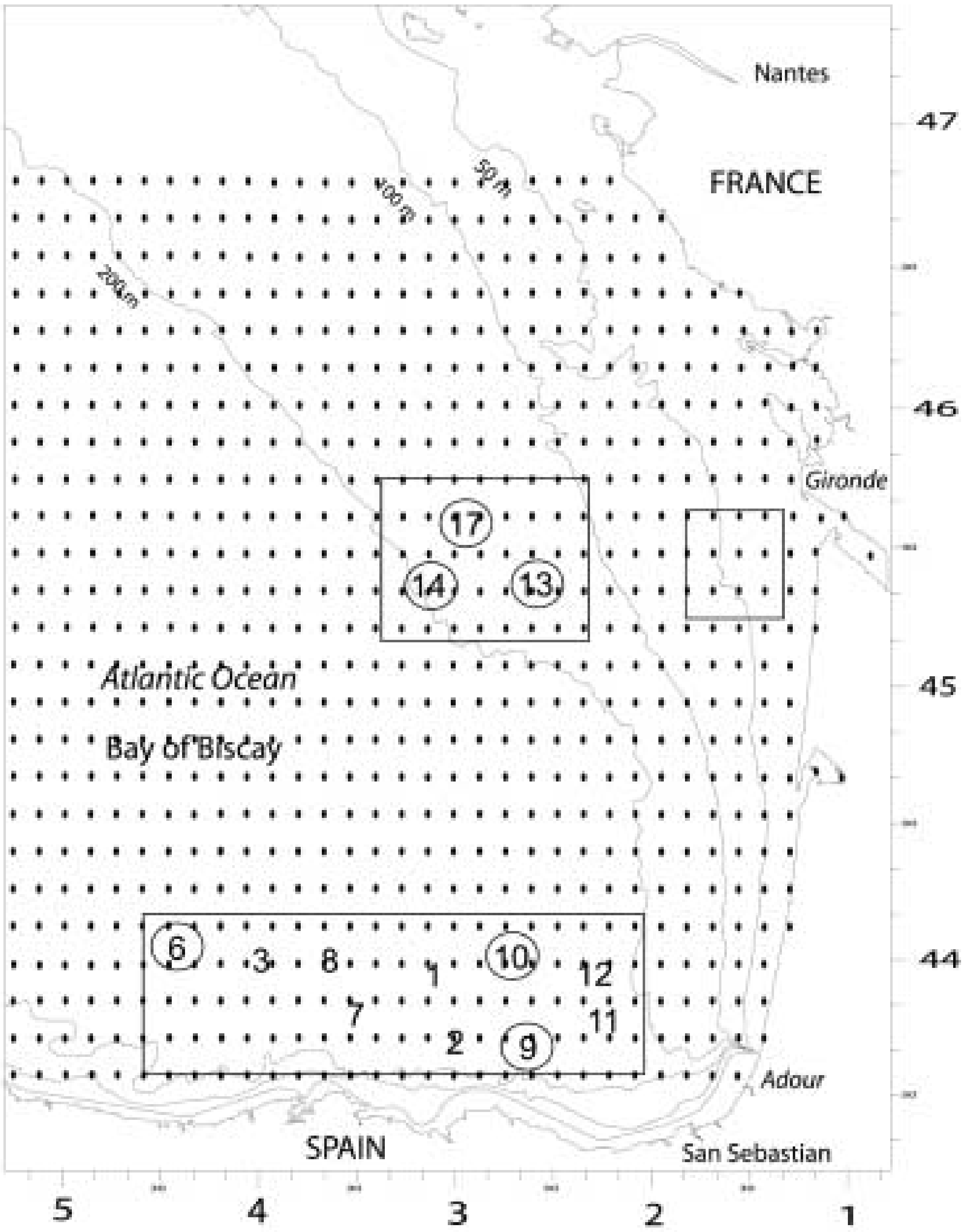

Figure 1: Starting locations (*points*) of the virtual buoys released weekly in the hydrodynamic model and synoptic description of the September 1999 juvenile survey in the Bay of Biscay (Juvesu survey performed by IFREMER and AZTI). The *rectangles* represent the surveyed areas. The *numbers* indicate the location and the serial number of the trawls with juvenile anchovies. The *circles* correspond to the samples of juveniles used for otolith microstructure analysis.

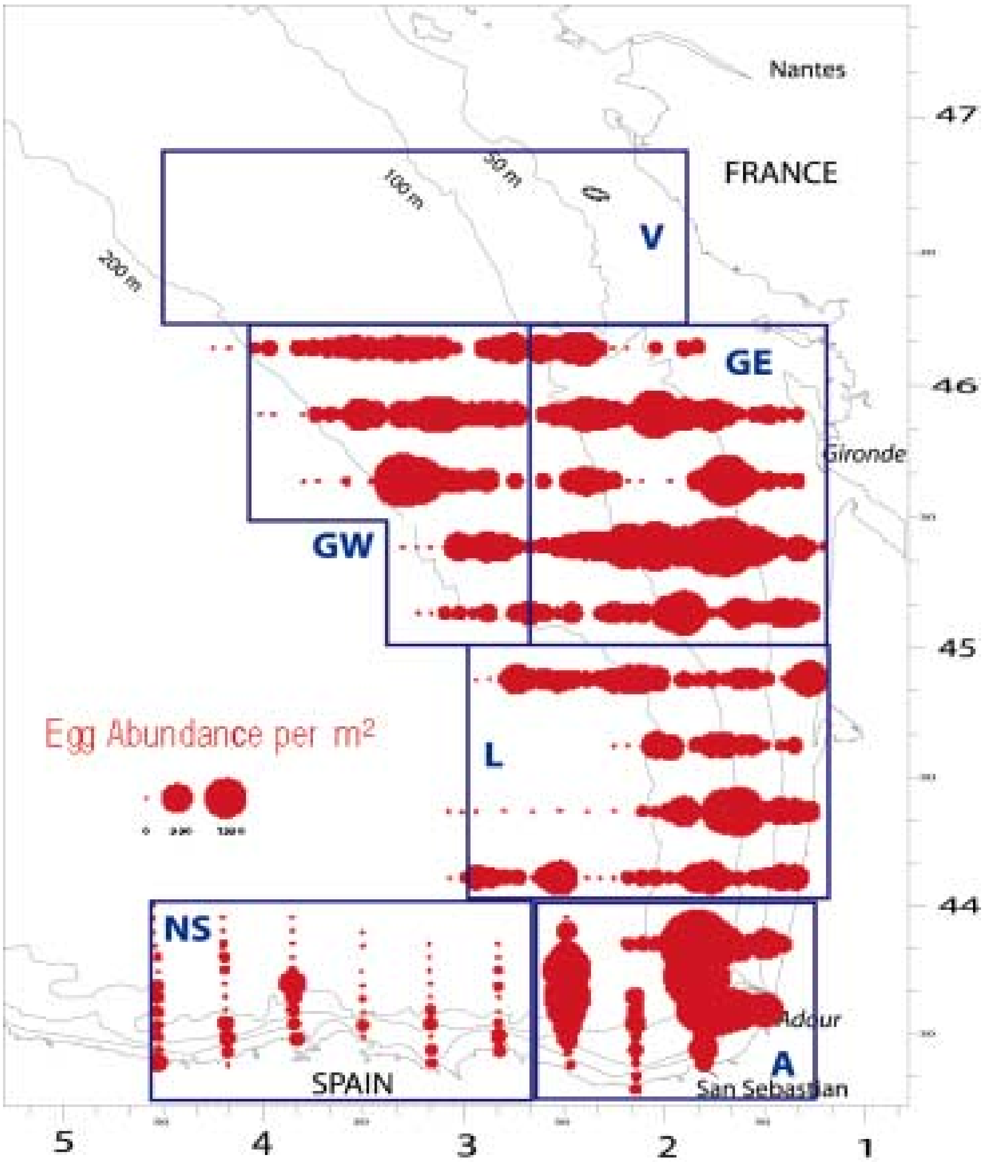

Figure 2. Distribution of anchovy eggs in May-June 1999 (BIOMAN survey performed by AZTI). The rectangles correspond to the spawning strata used in the transport model. *V*: Vendee, *GW*: Gironde West, *GE*: Gironde East, *L*: Landes, *A*: Adour, *NS*: North Spain.

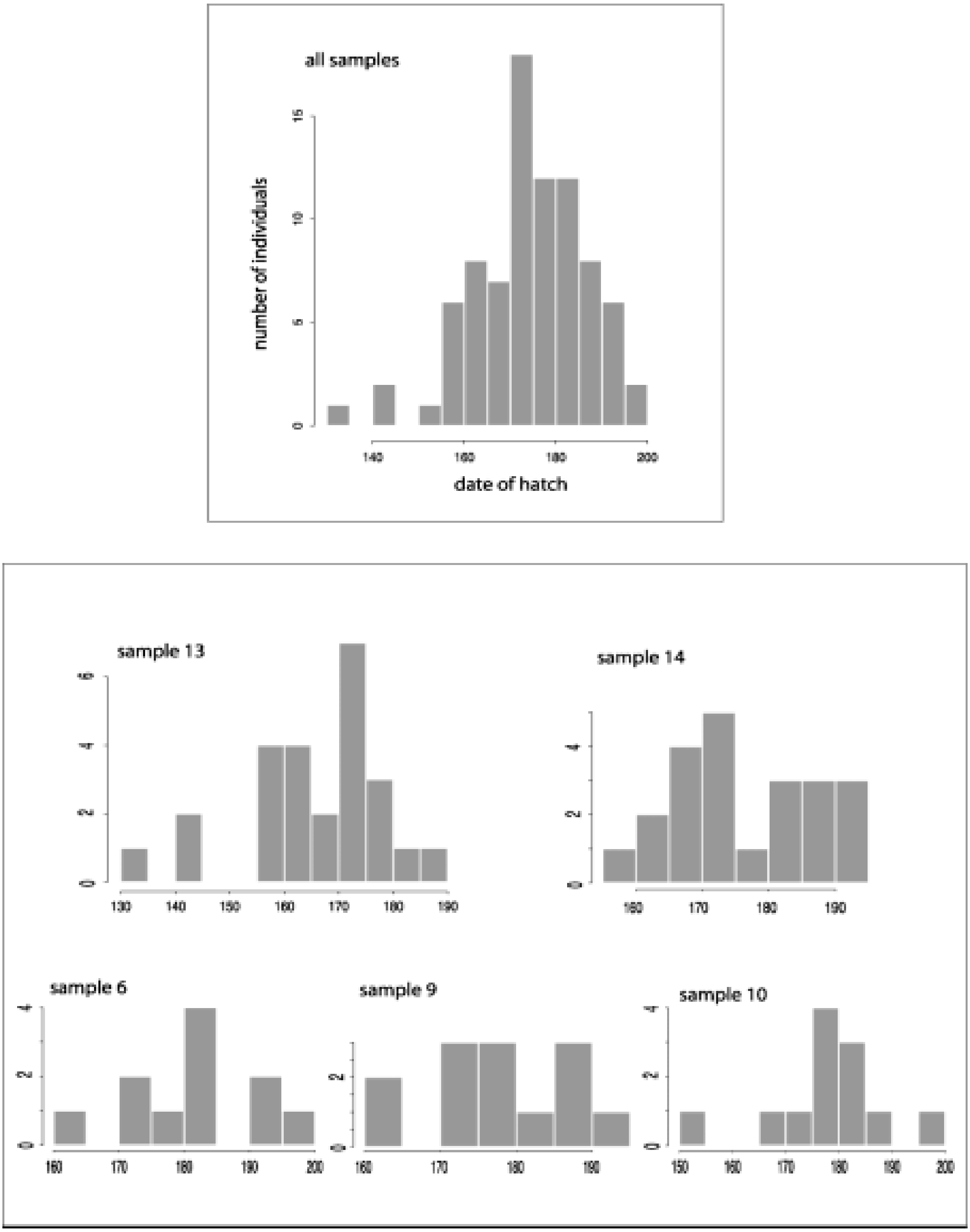

Figure 3 : Histograms of the hatching dates of juveniles sampled in September 1999, determined using otolith microstructure analysis. *Top* : all samples together. *Bottom* : by sample.

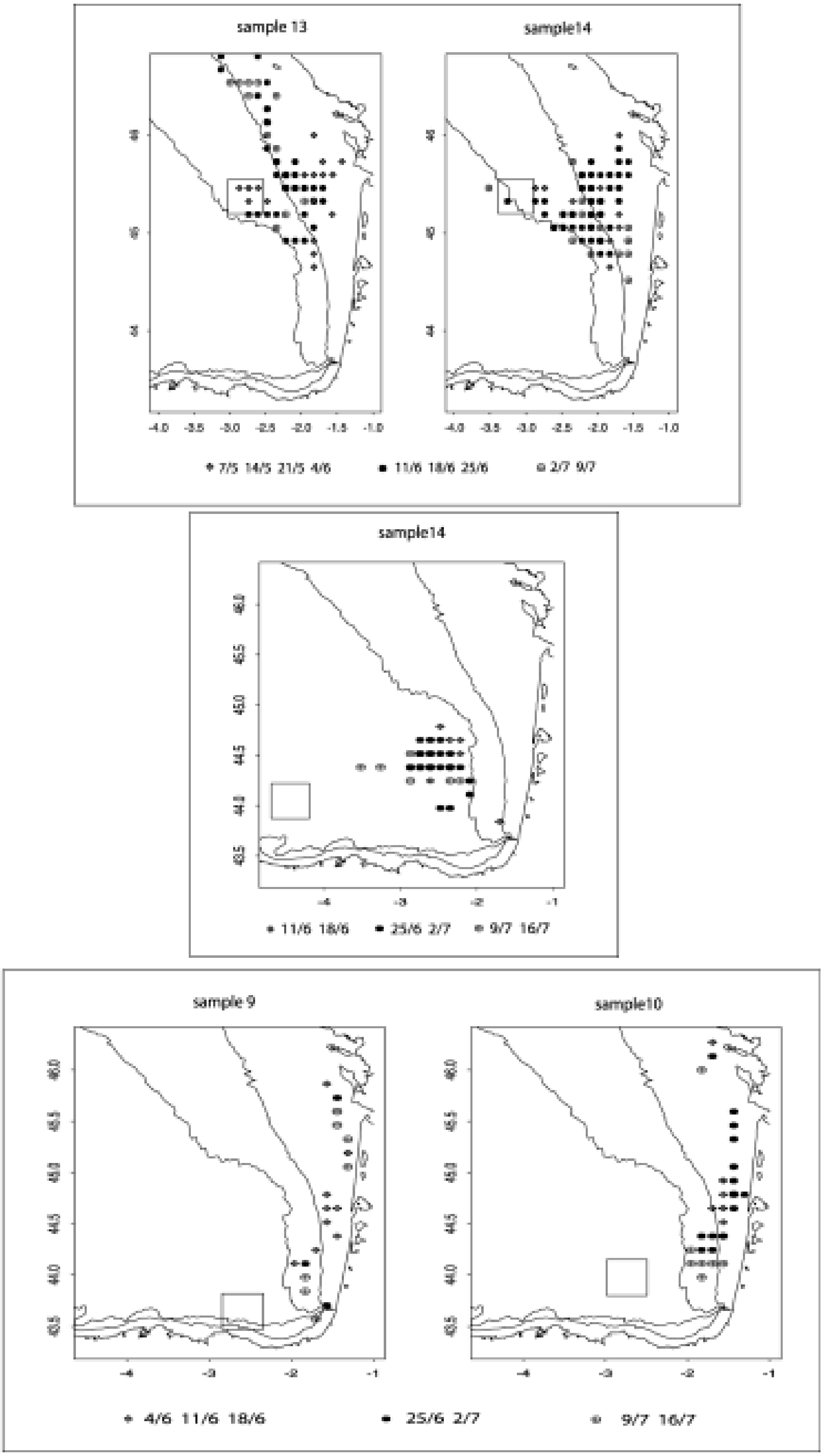

Figure 4 : Possible origin of juveniles sampled in September 1999 (five samples). The *squares* represent the areas where the juveniles were caught (see text). The *points* correspond to the possible locations of their hatching origin according to the transport model. The point symbols are related to the dates of the weekly releases of virtual buoys (black dots indicate the peak hatching period).

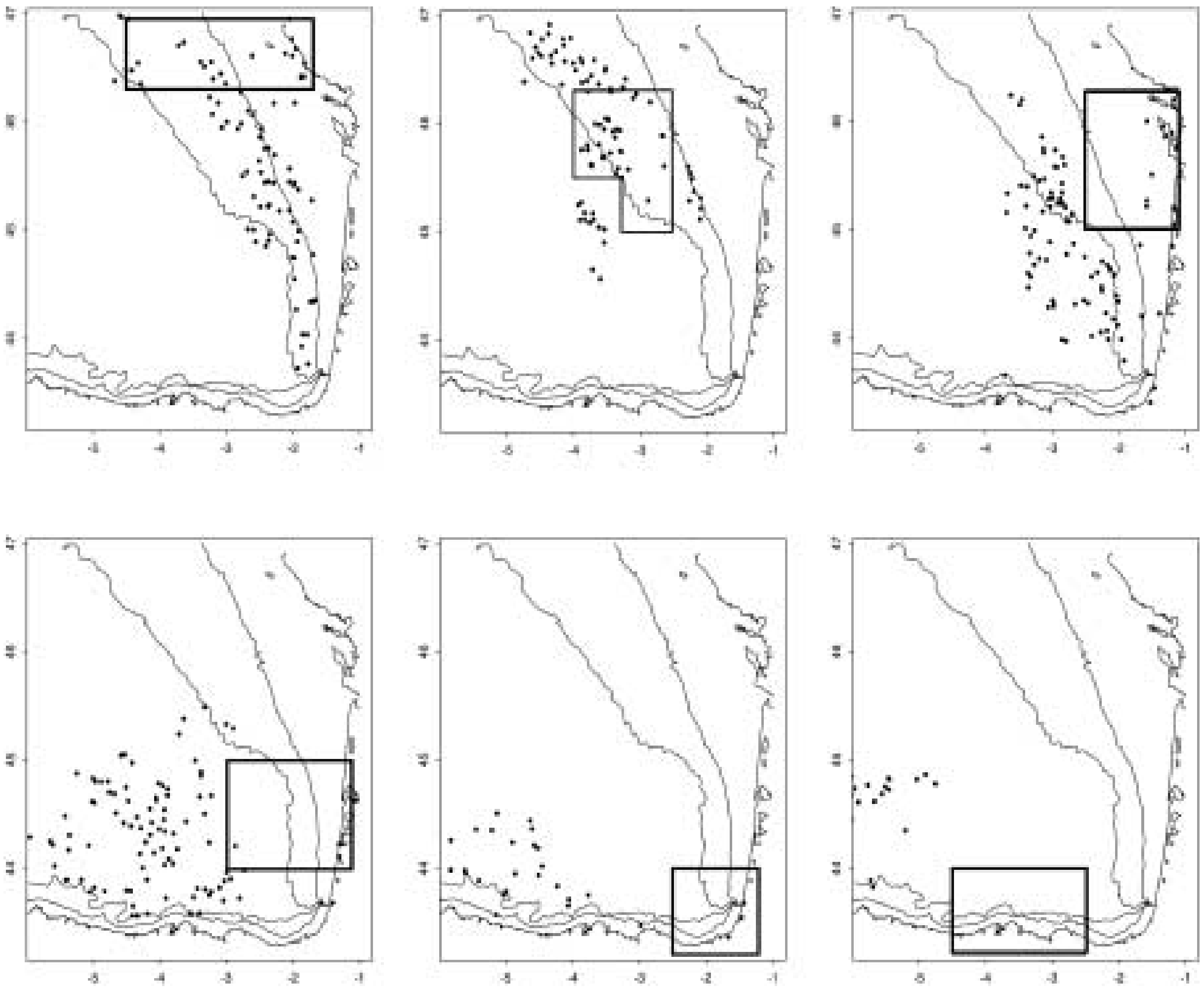

Figure 5 : Simulated location on 14 September 1999 (*points*) of the virtual buoys released on 25 June (peak hatching period of the sampled juveniles) in the different spawning strata (*rectangles*).

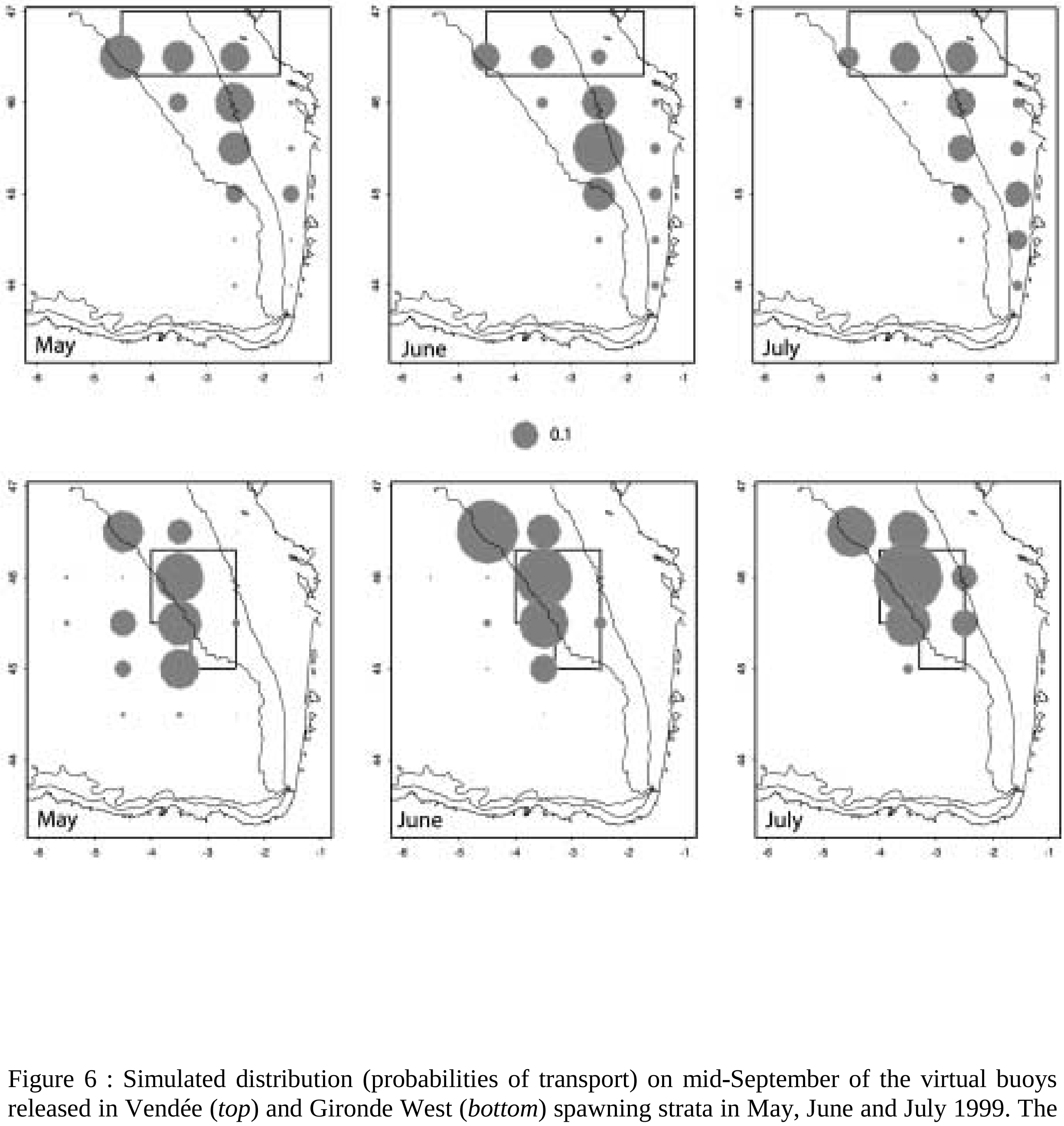

Figure 6 : Simulated distribution (probabilities of transport) on mid-September of the virtual buoys released in Vendée (*top*) and Gironde West (*bottom*) spawning strata in May, June and July 1999. The *rectangles* correspond to the limits of the spawning strata (see Fig. 2). The *circles* radius is proportional to the probability of transport from the spawning strata to the corresponding square of the grid.

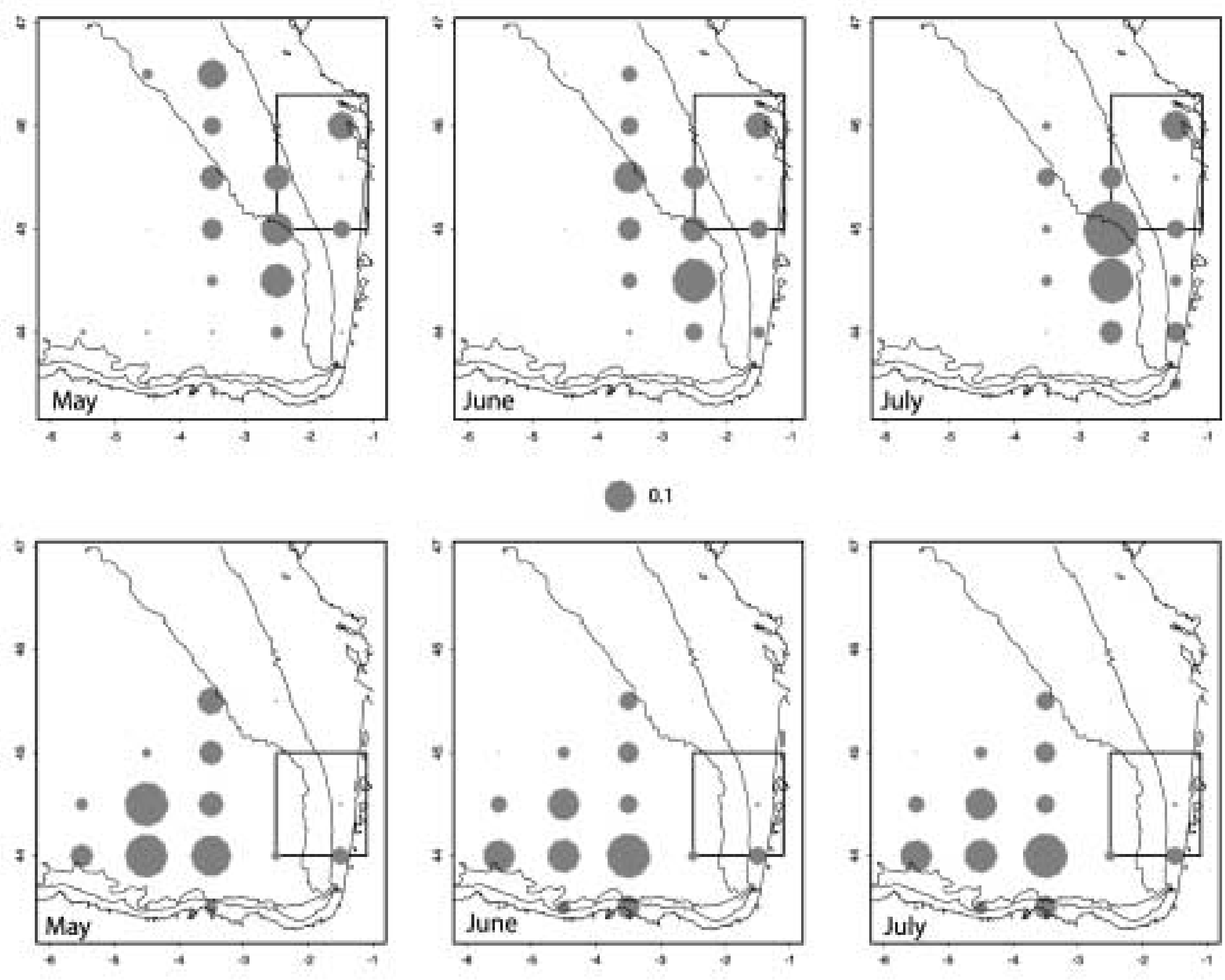

Figure 7 : Simulated distribution (probabilities of transport) on mid-September of the virtual buoys released in Gironde East (*top*) and Landes (*bottom*) spawning strata in May, June and July 1999. The *rectangles* correspond to the limits of the spawning strata (see Fig. 2). The *circles* radius is proportional to the probability of transport from the spawning strata to the corresponding square of the grid.

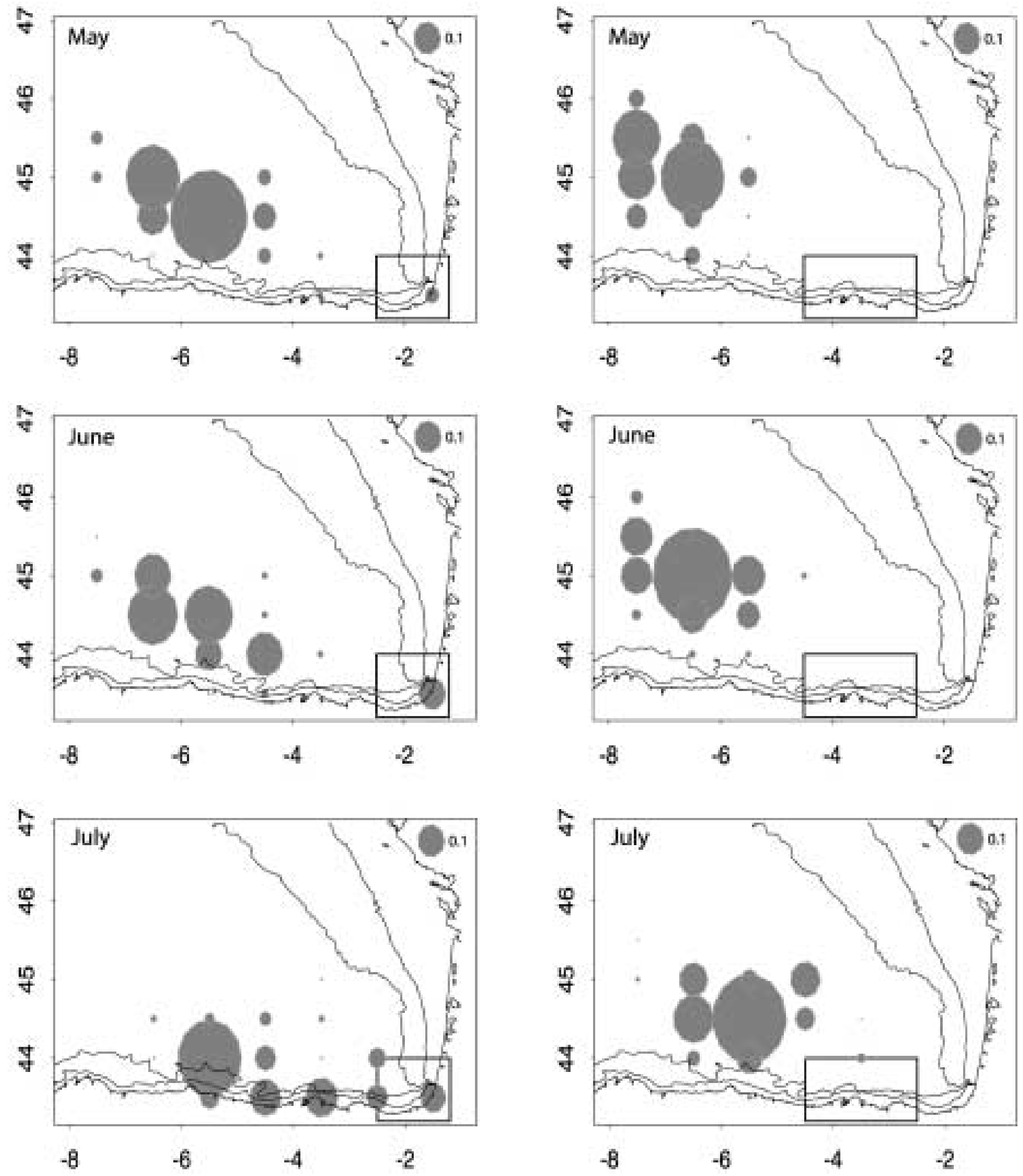

Figure 8 : Simulated distribution (probabilities of transport) on mid-September of the virtual buoys released in Adour (*top*) and North Spain (*bottom*) spawning strata in May, June and July 1999. The *rectangles* correspond to the limits of the spawning strata (see Fig. 2). The *circles* radius is proportional to the probability of transport from the spawning strata to the corresponding square of the grid.

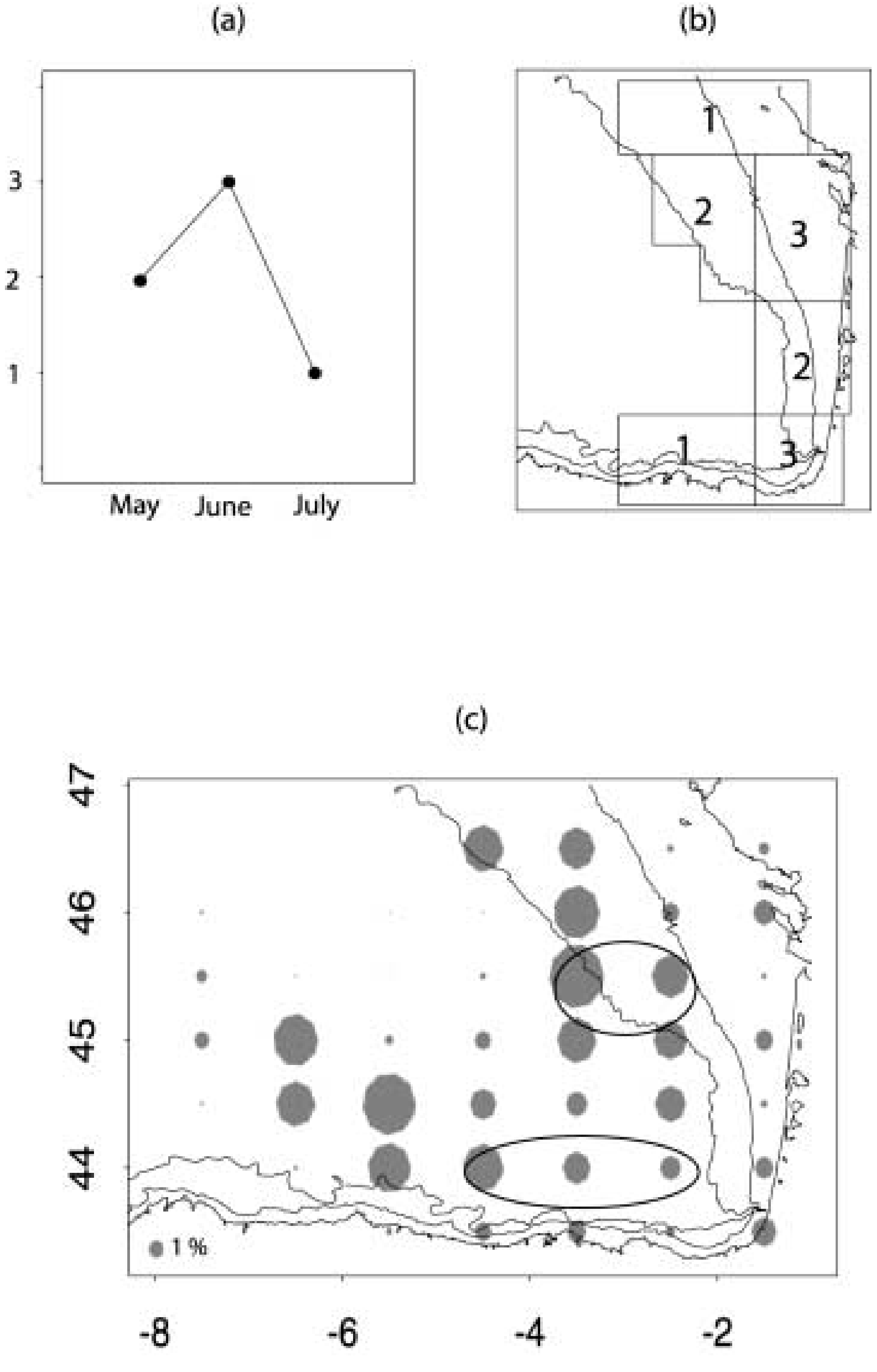

Figure 9 : Spawning model and subsequent juvenile distribution. The temporal *(a)* and spatial *(b)* coefficients used to reproduce anchovy spawning pattern in the Bay of Biscay. The probable spatial distribution of anchovy juveniles on mid-September 1999 *(c)* according to the spawning and transport models. The *circles* radius is proportional to the weighted probability of transport from the spawning strata of the virtual buoys released in May, June and July. The *ellipses* correspond to the areas where juveniles where caught during a survey in September 1999.

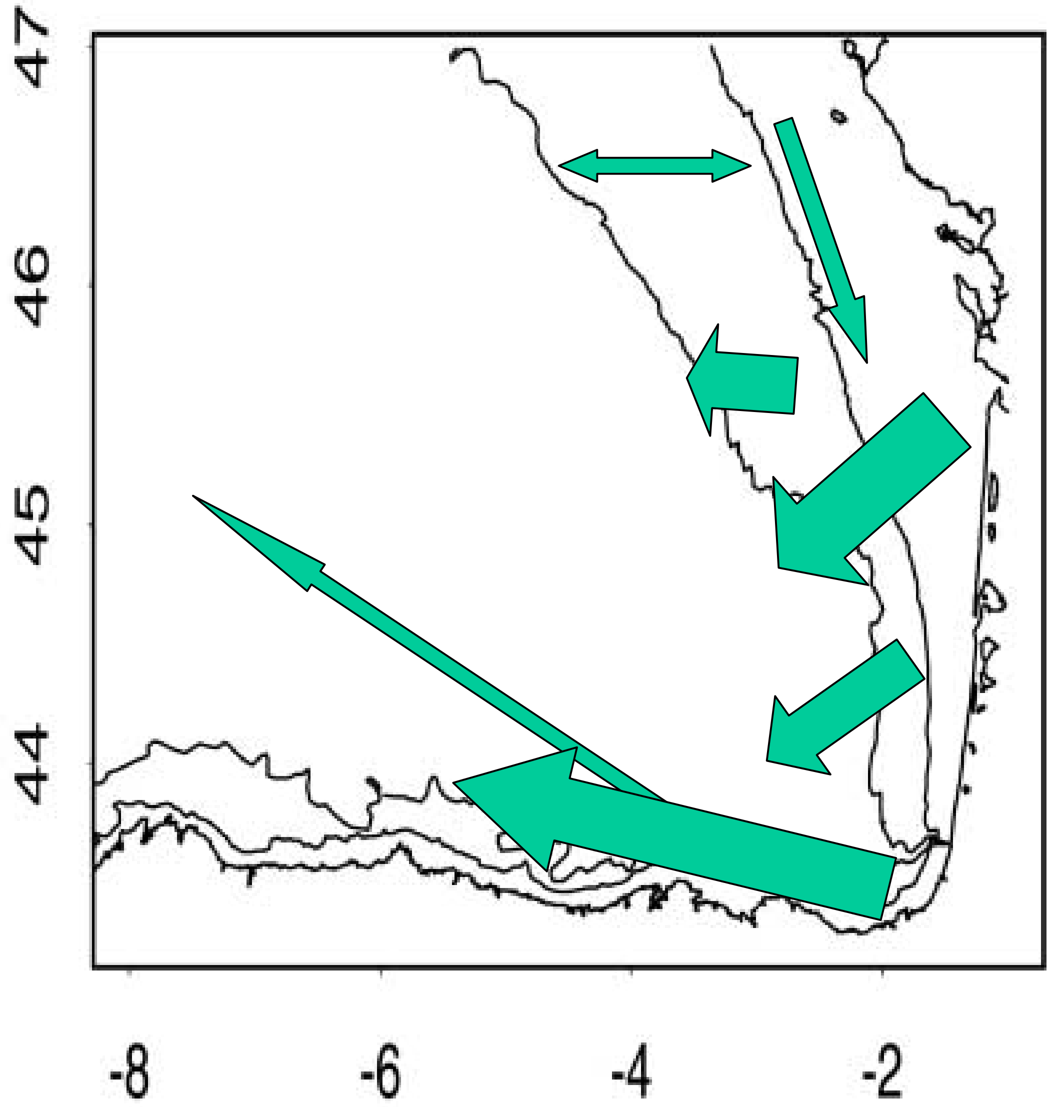

Figure 10 : Synoptic description of the simulated transport scheme affecting Biscay anchovy from the egg to the juvenile stages in 1999. The length of the arrows represents the distance from the spawning grounds to the supposed nursery grounds. The width of the arrows is related to the importance of the different spawning areas.

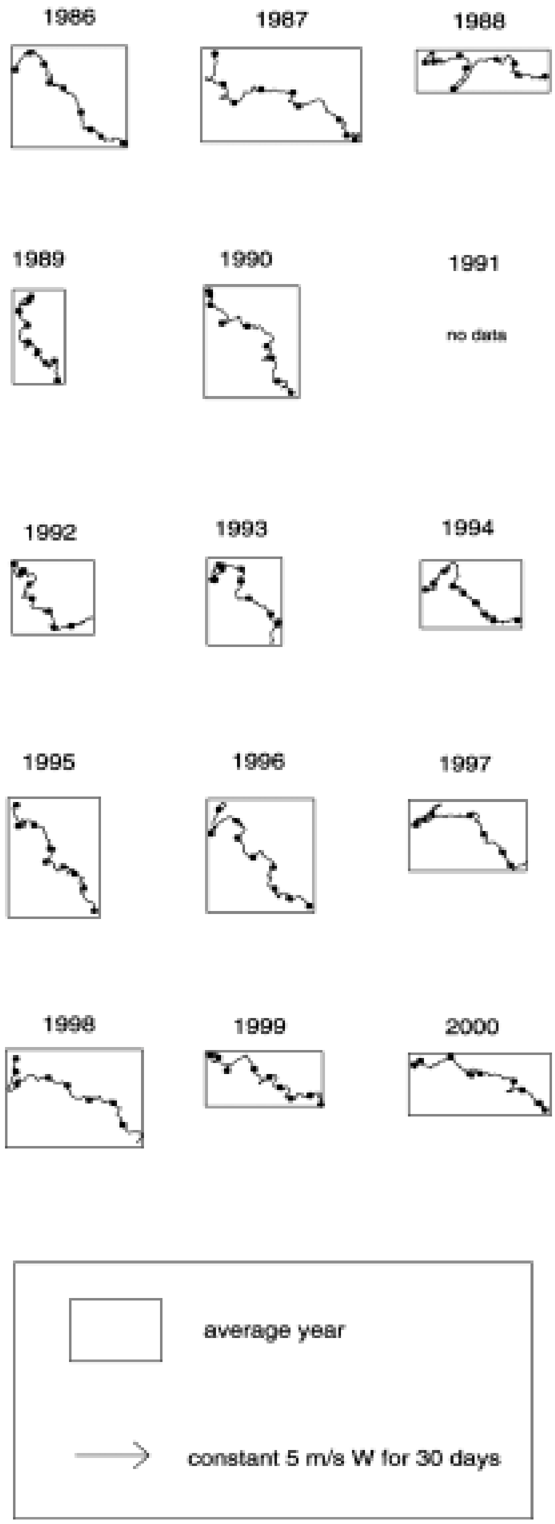

Figure 11 : Cumulative vector diagrams of wind stress from 1 May to 31 August at Chassiron semaphore (France) from 1986 to 2000. The interval between two black dots corresponds to 15 days of cumulated wind stress.

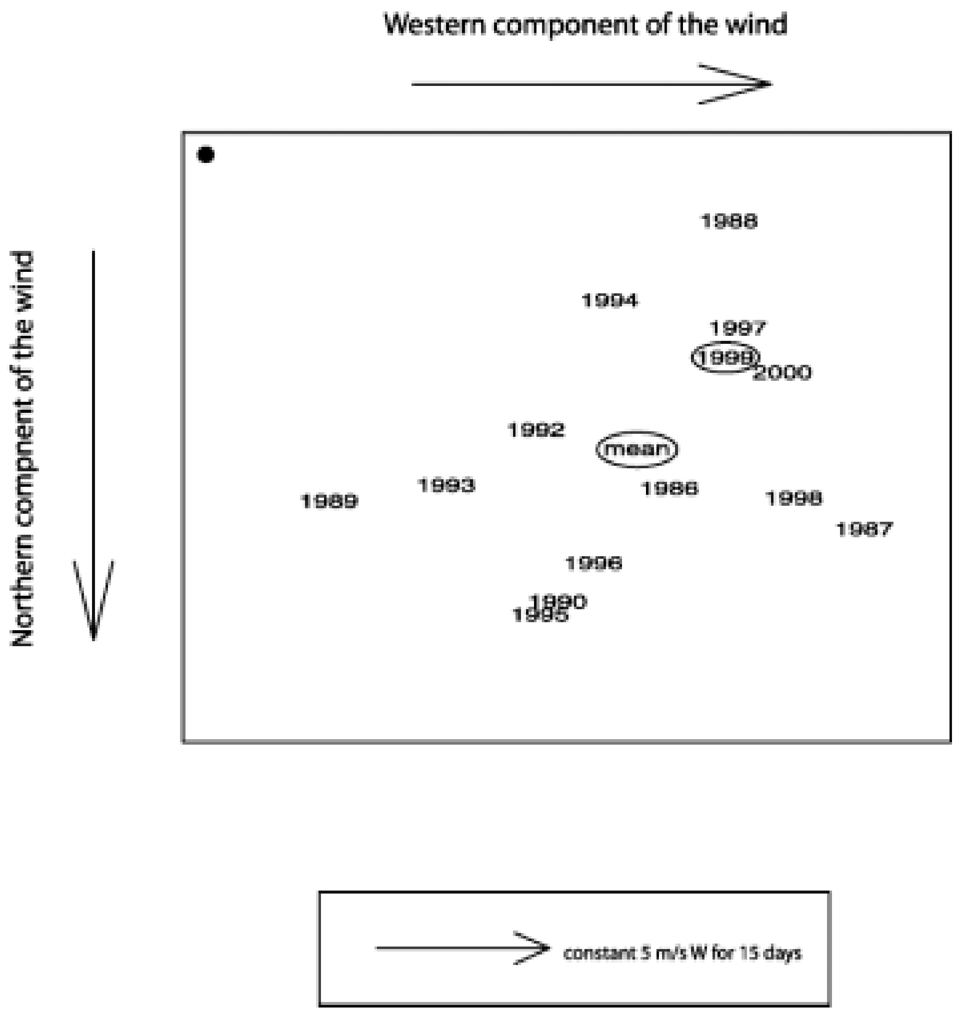

Figure 12 : Synthetic description of the cumulative vector diagrams of wind stress from 1 May to 31 August at Chassiron semaphore (France) from 1986 to 2000. The black dot represents the starting point on 1 May. The arrival point on 31 August is indicated for each year and the mean year over the series.