

**Comparative otolith growth and drift of larval and juvenile anchovy in Biscay
and implications for survival**

by

G. Allain, P. Petitgas, P. Grellier and P. Lazure

In spring 1999, repeated larval surveys were undertaken by IFREMER from March to July on a major spawning ground of anchovy off Gironde estuary. In September, a juvenile survey was performed in collaboration with AZTI. The paper describes the methodology for reading the larval and juvenile otoliths as well as for reconstructing the correspondence in space and time between juveniles and larvae using a 3D hydrodynamic model. The thin otoliths (sagittae) of the larvae were read directly using a light microscope. The thicker otoliths (sagittae) of the juveniles had to be polished before reading. To read the narrow increments near the nucleus (first weeks after mouth opening), it was necessary to use a greater magnification (x1250) than for the overall reading (x312.5). Because the otolith increases along preferential axes after larval stage, measurements were always performed in a similar manner relative to these axes. Virtual buoys were released in the hydrodynamic model on a regular grid at dates compatible with the estimated juvenile birthdates. The trajectories that arrived near juvenile sampling locations at dates compatible with sampled juvenile ages were retained and their origin was thus evidenced. Some of the juveniles sampled in September could have originated from the French spawning ground off the Gironde estuary in June and July. The comparison of the survived juvenile growth rates during their larval period with the otolith growth rate of the June and July larvae supported the idea of growth-selective survival : the survived September juveniles showed faster growth than the pool of June larvae they were estimated to originate from. Variations in otolith growth pattern also suggest a higher juvenile growth over the shelf break than in oceanic waters.

Keywords : growth, otolith, selection, survival, larva, juvenile, anchovy, transport, Biscay.

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INTRODUCTION

Marine fish experience high rates of mortality during their larval and juvenile life. A common hypothesis suggests that the fastest growing individuals are more likely to survive than the slow growing ones (Houde 1987, Bailey & Houde 1989). The fast growing individuals would be exposed for a shorter 'critical' period to the hazards of larval life (i.e. reduced mobility, high vulnerability to predation and turbulence). The "bigger-is-better" hypothesis has been tested in rearing experiments (Rosenberg & Haugen 1982, Leggett & Deblois 1994), more rarely in the field (Hovenkamp 1992, Meekan & Fortier 1996, Sogard 1997) due to the difficulty of collecting juveniles and larvae representative of the same original population.

In this study, the time origin (birthdate) of larval and juvenile anchovies collected in Biscay in 1999 was determined using otolith microstructure examination and their spatial origin was studied using a 3D hydrodynamical model (cf. Allain et al. 2001). Larvae and juveniles with the same spatio-temporal origin were selected and supposed to belong to the same micro-cohorts. Their individual growth histories were then compared to investigate the selection process.

MATERIALS AND METHODS

Determination of birth dates and growth curves using otolith microstructure analysis

Larvae : In spring 1999, monthly egg and larval surveys were undertaken by IFREMER with its R/Vs "Gwen Drez" and "Thalia", from March to July on a major spawning ground of anchovy *Engraulis encrasicolus* off Gironde estuary (program PLAGIA). Larvae were sampled with towed hauls at 2 knots using the "Carré Net" (Bourriau, 1991) mounted with a 315 μm mesh. 16 hauls were performed each month on the same grid (cf. Fig 1). 102 larvae collected on 26-27 May, 23-25 June and 12-15 July were analysed.

The thin otoliths (sagittae) of the larvae were read directly using a light microscope at magnification $\times 1250$. The age of each larva 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 larvae were 6 to 20 days old after hatching. Date of hatch was then deduced from the age estimated and the date of sampling. Otolith width was measured every five increments from the innermost increment to the edge of the otolith. Growth rate (mm day^{-1}) was defined as the measured otolith width divided by the number of daily increments corresponding to the measured width. Otolith growth was adopted as a proxy measurement for somatic growth (Garcia *et al.*, 1998).

Juveniles : In September 1999, an acoustic survey targeting juvenile anchovy was jointly conducted by IFREMER and AZTI as part of the European project JUVESU with the IFREMER R/V "Gwen Drez". The following areas were surveyed: SE Biscay, Spanish coast and continental shelf off Gironde. These areas are known as potential nursery grounds for juvenile anchovy *Engraulis encrasicolus*. Juveniles were sampled at sea surface (0-20 m) using a mid-water pelagic trawl mounted with a 4 cm mesh in the codend and hauled at 3-4 knots. 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 thicker otoliths (sagittae) of the juveniles had to be polished before reading. To read the narrow increments near the nucleus (first weeks after mouth opening), it was necessary to use a greater magnification ($\times 1250$) than for the overall reading ($\times 312.5$), cf. Fig. 2 (cf. Campana et al. 1987). The juveniles were 54 to 128 days old after hatching. Because the otolith increases along preferential axes after larval stage, measurements were always performed in a similar manner relative to these axes. As for the larvae, the age of each juvenile was counted in daily increments from the mark of mouth opening. The date of hatch was deduced from the age estimated and the date of sampling (Fig. 3).

Otolith width was also measured every five increments from the inner-most increment to the edge of the otolith. Growth rate (mm day^{-1}) was defined as the measured otolith width divided by the number of daily increments corresponding to the measured width.

The otolith growth curves of the larvae and juveniles were plotted against age (cf. Fig. 4).

Tracking of water masses trajectories in a 3D hydrodynamic model

A 3D circulation model for the whole Bay of Biscay (Allain et al. 2001; Jégou *et al.*, in press) 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 corresponded to the whole Bay of Biscay. The model used here was a new model in comparison the former model which was limited to Biscay French continental shelf (Jégou and Lazure, 1995; Lazure et Jégou, 1998). The model used here extended 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 $5 \text{ km} \times 5 \text{ km}$ 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).

Anchovy larvae and juveniles were found in the surface layer (0-30 m) mainly above the thermocline during the surveys. Anchovy larvae were reported to 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.

Selection of juveniles and larvae with the same spatio-temporal origin

Selection in space : Virtual buoys, marking unit water masses, were released on a $10 \text{ km} \times 10 \text{ km}$ grid south of 47°N (cf. Fig. 1) every week during the hatching period of the sampled juveniles and larvae (i.e. May to July, cf. Fig. 3). The buoys trajectories were stopped on the juvenile sampling dates (mid-September). Those trajectories were selected which began during the hatch period of a given sample of larvae/juveniles and ended in their sampling area at sampling dates. They represented the trajectories potentially experienced by the larvae/juveniles during their early life. Individuals from the egg to the juvenile stages were considered to be transported passively by the average currents in the 30 m surface layer.

The arrival box for the larvae samples corresponded to the sampling area of the larvae off Gironde (cf. Fig. 5). The arrival box for a given sample of juveniles was defined by a square centred on the mean position of the related trawl haul. The square dimension was 21×21 nautical miles (approx. 0.5° in longitude) (Fig. 6). The starting locations of the selected trajectories corresponded to the hatching area of the larvae/juveniles according to the transport model.

One trajectory was selected for each individual juvenile among the trajectories related to its sample. It was defined as the trajectory beginning on its hatching week and ending at the minimum distance of its sampling location on the sampling date. If the starting point of the trajectory was located within the potential hatching area of the larvae, then the juvenile was selected.

Selection in time : The hatching dates of the selected juveniles were compared with those of the larvae. The selected juveniles and larvae born in the same week were considered to belong to the same micro-cohort. A micro-cohort was constituted by all the individuals born at the same period in the same area and consequently subject to the same environmental conditions. The juveniles were then considered as the possible survivors of the mortality process that affected the micro-cohort of larvae.

The growth characteristics of the larvae and juveniles belonging to the same micro-cohorts were compared to investigate the selection process.

Last, the growth pattern of the juveniles was related to their drift pattern in the Bay of Biscay.

RESULTS AND DISCUSSION

Connection in space and time of the larvae and juveniles

The potential hatching area of the larvae largely overlapped the sampling area off Gironde because of the limited drift of the larvae in their first weeks (Fig. 5). This hatching area is limited by the latitudes (45°N, 46.5°N) and longitudes (2.2°W, 1°W). The potential hatching area of the juveniles (Fig. 6) partly overlapped this "larval" box, except for the case of sample 6 (not illustrated).

46 juveniles sampled over the French break and off the Spanish shelf-break were selected. The starting points of their individual trajectories were located within the hatching area of the larvae sampled off Gironde (45°N, 46.5°N, 2.2°W, 1°W), according to the transport model.

The hatching dates of these juveniles were compared to those of the larvae (Fig. 3). Only one individual was born during the hatching period of the May sample of larvae (7-18 May). 18 juveniles were born during the hatching period of the June sample of larvae (4-20 June). 25 juveniles were born during the hatching period of the July sample of larvae (24 June-10 July).

A compromise had to be found between the precision of the selection in space and time of the larvae and juveniles and the number of individuals selected in each micro-cohort. Therefore two micro-cohorts were considered: one formed by the individuals born from 4 to 20 June off Gironde (21 larvae, 18 juveniles) and a second one formed by the individuals born from 24 June to 10 July off Gironde (24 larvae, 25 juveniles).

Growth-selective mortality between larval and juvenile stages

The otolith growth rates of the larvae and juveniles from the two micro-cohorts are plotted on Figure 7. The figure showed a difference between the distributions relative to the larvae and the juveniles at a given age. The otolith growth rates of the juveniles were higher than those of the larvae. This shift appeared in the first five days (Fig 7a) or ten days (Fig 7b) after hatching and increased with age.

These observations suggested the existence of a growth-selective mortality between larval and juvenile stages in the field. The faster growing individuals would have a better chance to survive. The factors implied in growth selective mortality include vulnerability to predation and duration of larval 'critical' stages (Meekan & Fortier 1996).

Growth and drift patterns of the juveniles

The otolith growth curves of the juveniles (Fig. 4) showed a similarly increasing growth rate until the age of 40 to 60 days after hatching, which corresponded to the period of metamorphosis (Ré 1986). After this transition, the otolith growth rate declined. This decline varied between individuals. On average, the decline was earlier and stronger for juveniles from samples 6, 9 and 10 than for juveniles from samples 13 and 14 (Fig. 4).

The possible locations of the juveniles from the age of 40 days to the age of sampling (mean positions every five days of the trajectories selected in the transport model for each individual juvenile) are plotted on Figure 8. The juveniles from samples 13 and 14 were subject to low or retentive currents over the outer shelf and shelf break north of 45°N. The juveniles from samples 6, 9 and 10 were transported in oceanic waters off the shelf break south of 45°N.

Variation in the growth pattern of juveniles corresponds to differences in their drift pattern. The otolith growth rate during and after metamorphosis must be influenced by the environment experienced by the juveniles along their trajectories. These observations suggest that waters over the outer shelf and shelf break might be more favorable for juvenile growth than oceanic waters.

CONCLUSION

The paper presented the methodology used to compare the otolith growth histories of field-collected larvae and juveniles representative of the same micro-cohorts. 3D hydrodynamic modelling was necessary to select the larvae and juveniles with the same origin. The results suggested the existence of a growth-selective mortality between larval and juvenile stages. The otolith growth pattern of the juveniles seemed to be habitat-dependent.

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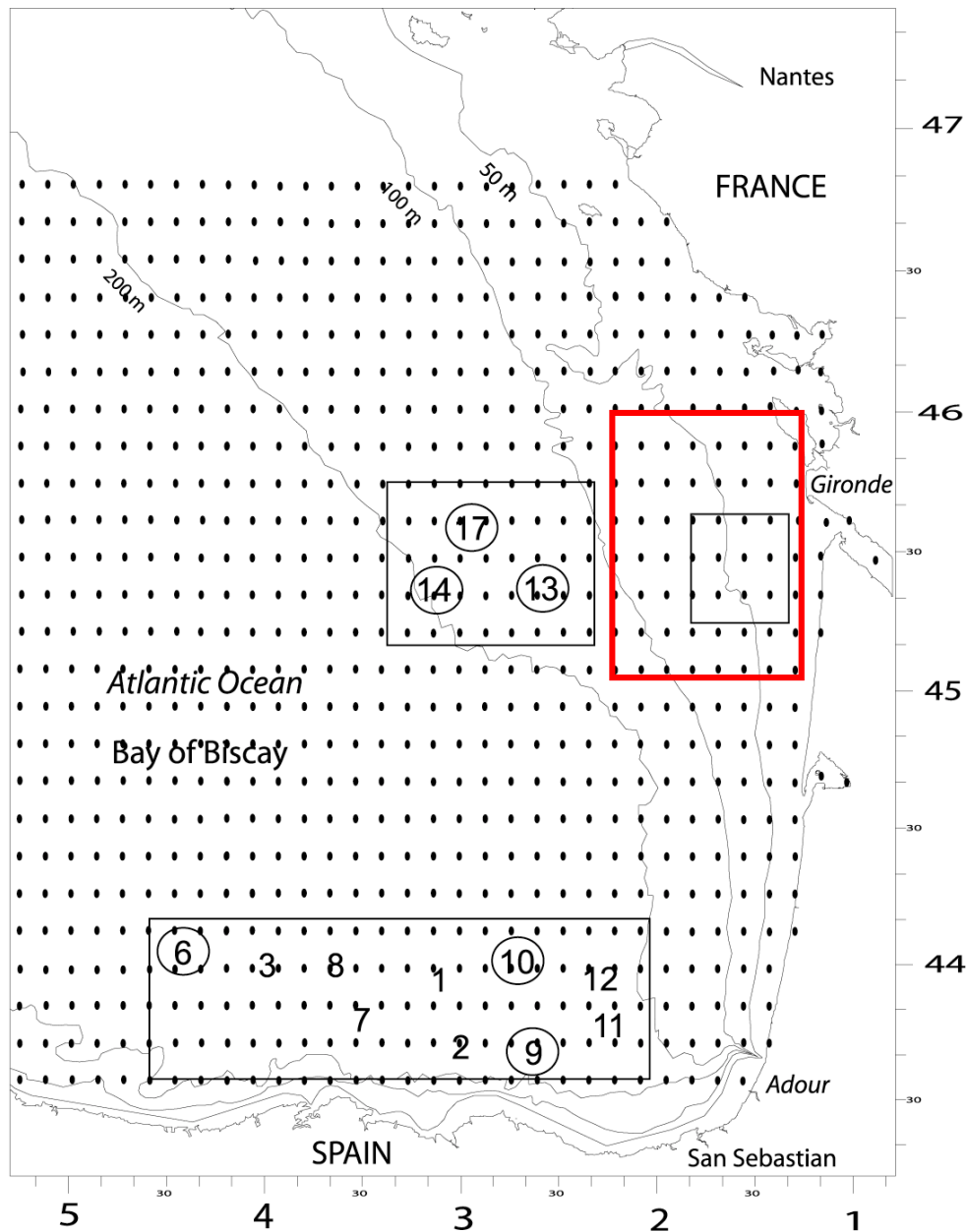


Figure 1: Starting locations (*points*) of the virtual buoys released weekly in the hydrodynamic model and synoptic description of the September 1999 juvenile survey in the Bay of Biscay (Juesu survey performed by IFREMER and AZTI). The *black rectangles* represent the surveyed areas. The *numbers* indicate 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. The red rectangle represent the area of larval surveys in May, June and July 1999 (Plagia surveys performed by IFREMER).

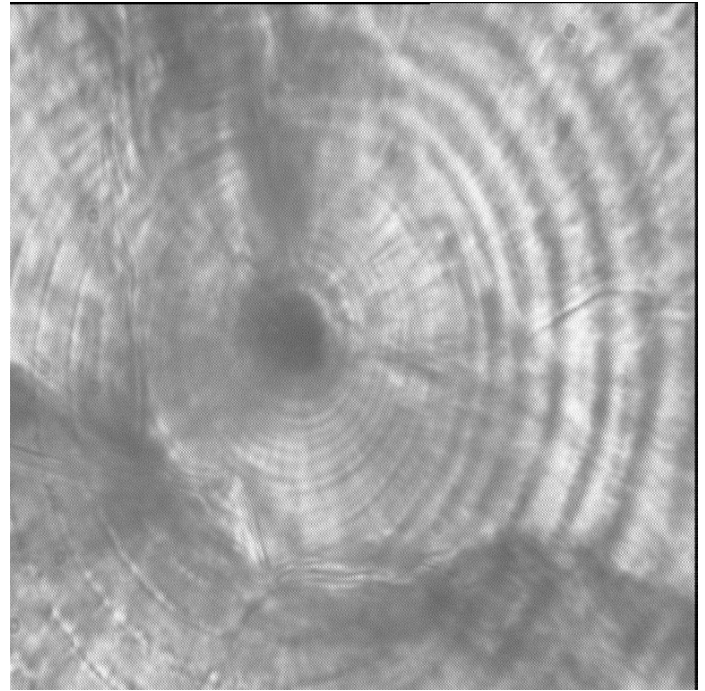
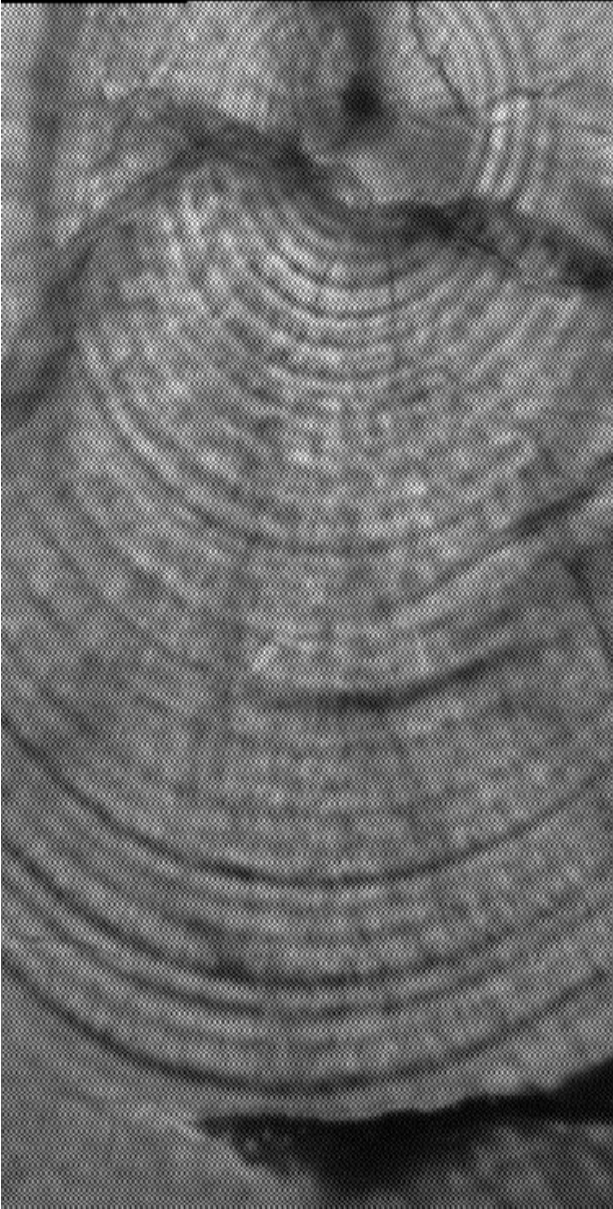


Figure 2. Two photographs of the same otolith (sagitta) of a juvenile anchovy collected in the Bay of Biscay in September 1999 and polished. *Left* : Magnification x312.5 used for the overall measurement of the daily increments. Growth axes appear after 25-30 days. *Right* : Magnification x1250 used to read the narrow increments near the nucleus (first weeks after mouth opening). Photos taken by P. Grellier.

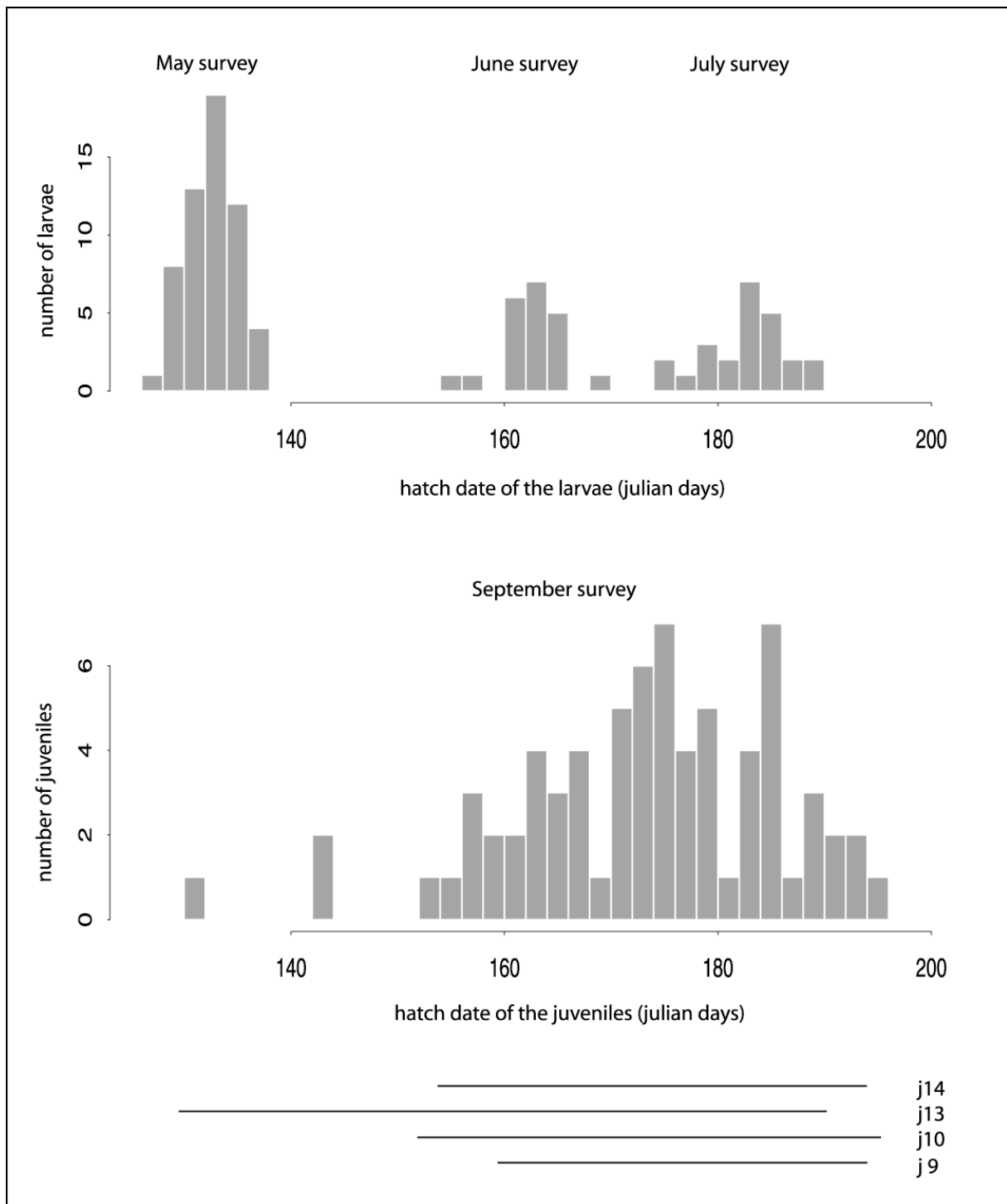


Figure 3 : Histograms of the hatching dates of larvae sampled in May, June and July 1999 (*top*) and juveniles sampled in September 1999, determined using otolith microstructure analysis (*bottom*). The hatching periods of the different juvenile samples are indicated below the histogram.

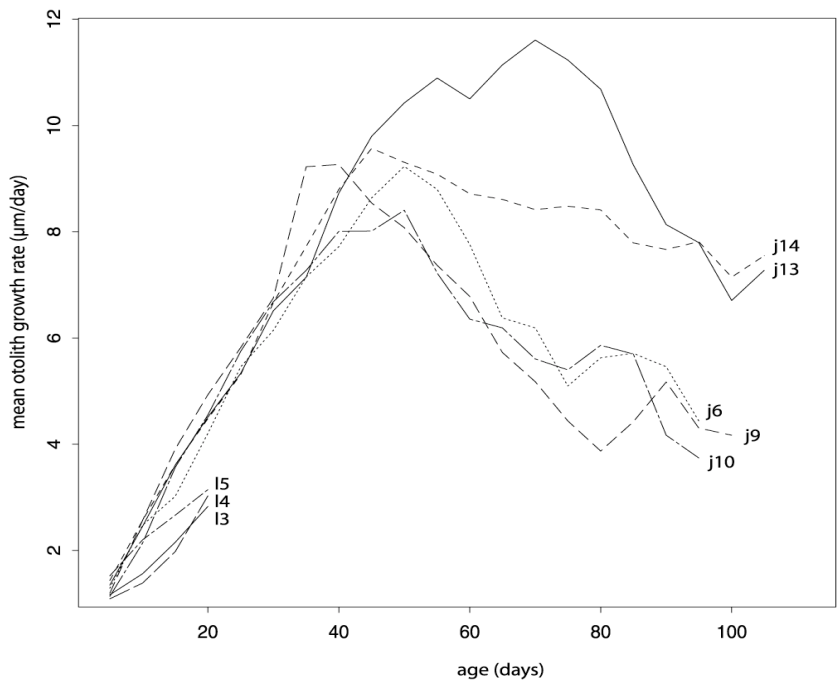


Figure 4 : Average otolith growth rate of anchovy larvae and juveniles by sample over periods of five days. *l3, l4, l5* : samples of larvae collected in May, June and July 1999 in the Gironde area. *j6, j9, j10* : samples of juveniles collected in September 1999 off the Spanish shelf break (see Fig.1). *j13, j14* : samples of juveniles collected in September 1999 over the French shelf (see Fig.1). Age is counted in days after hatching.

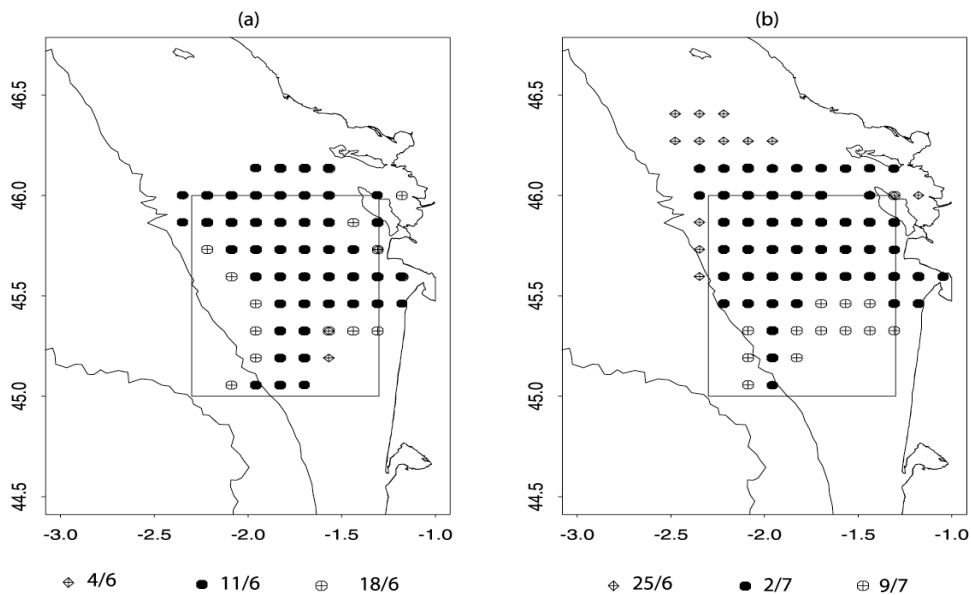


Figure 5 : Possible origin of the larvae sampled in June (a) and July (b) 1999. The *rectangles* represent the area where the larvae were caught (see text). The *points* correspond to the possible locations of their hatching origin according to the transport model. The point symbols are related to the dates of the weekly releases of virtual buoys.

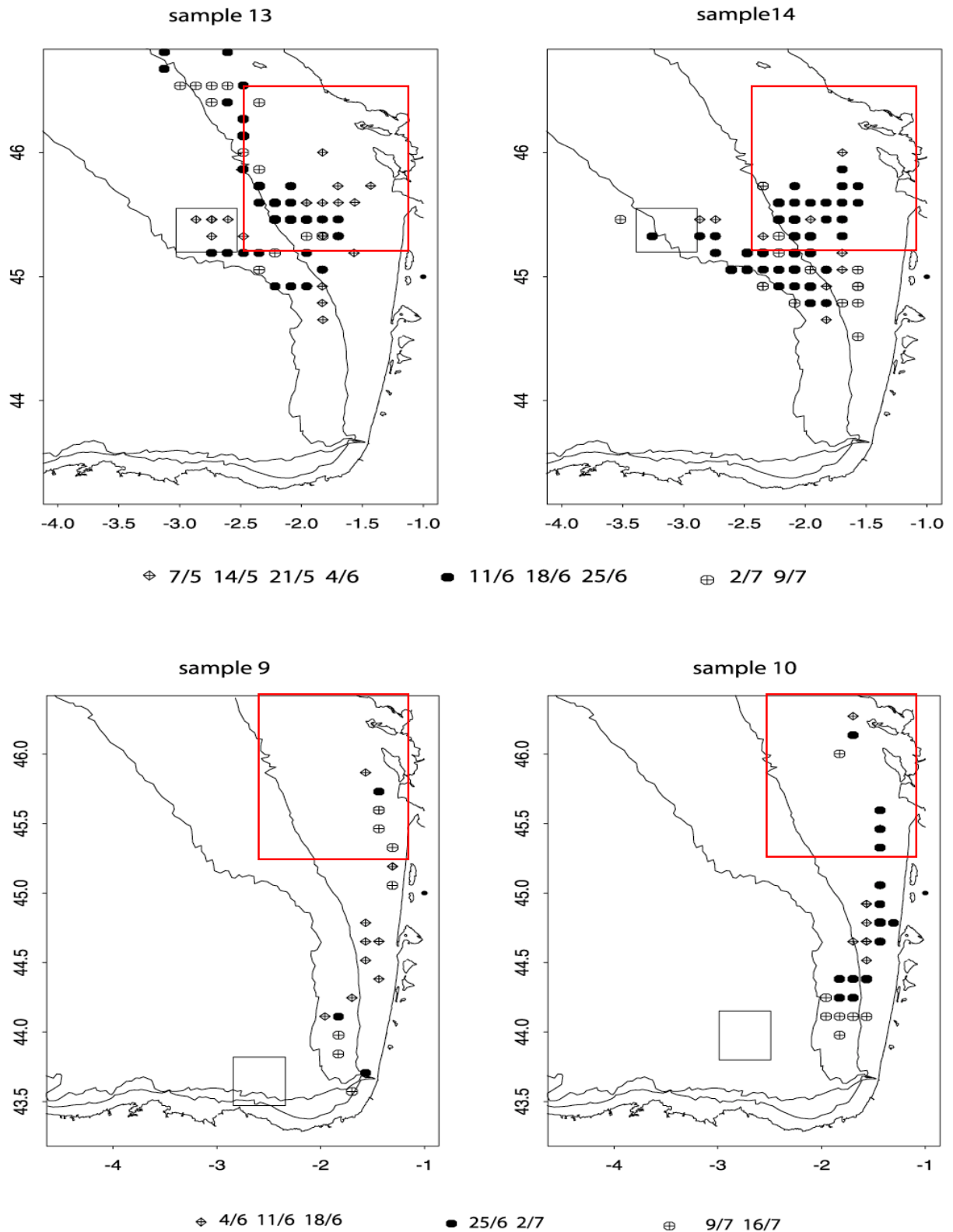


Figure 6 : Possible origin of the juveniles sampled in September 1999 (four samples). The *squares* represent the areas where the juveniles were caught (see text). The *points* correspond to the possible locations of their hatching origin according to the transport model. The point symbols are related to the dates of the weekly releases of virtual buoys. The *red rectangles* represent the hatching area of the larvae collected in May and June 1999 according to the transport model (see Fig. 4).

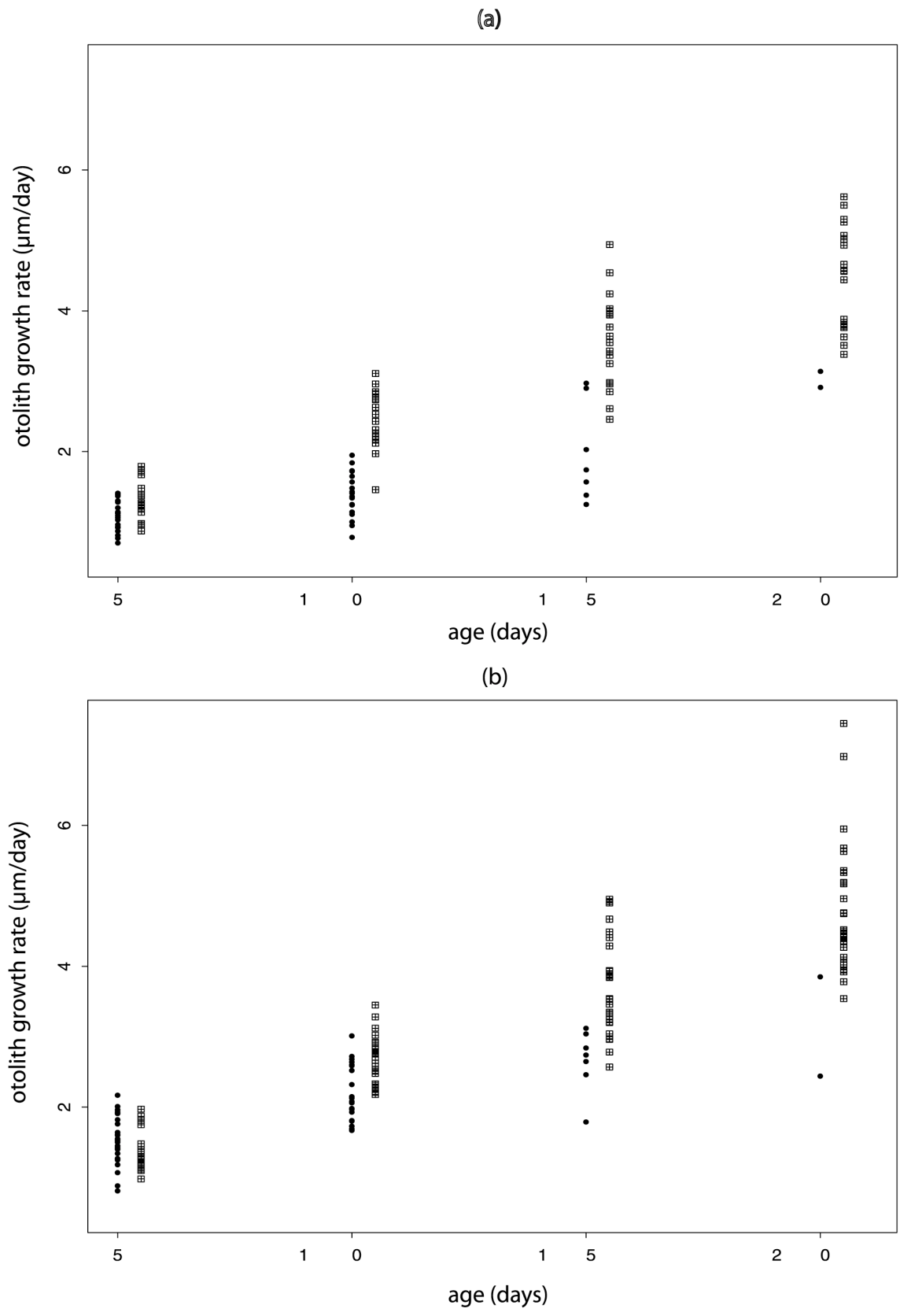


Figure 7 : Otolith growth rates of larvae (dots) and juveniles (squares) with the same spatio-temporal origin according to the transport model. (a) Larvae and juveniles hatched from 4 to 20 June in the Gironde area. (b) Larvae and juveniles hatched from 24 June to 10 July in the Gironde area. Age is counted in days after hatching. Otolith growth rate is calculated by five-increment periods.

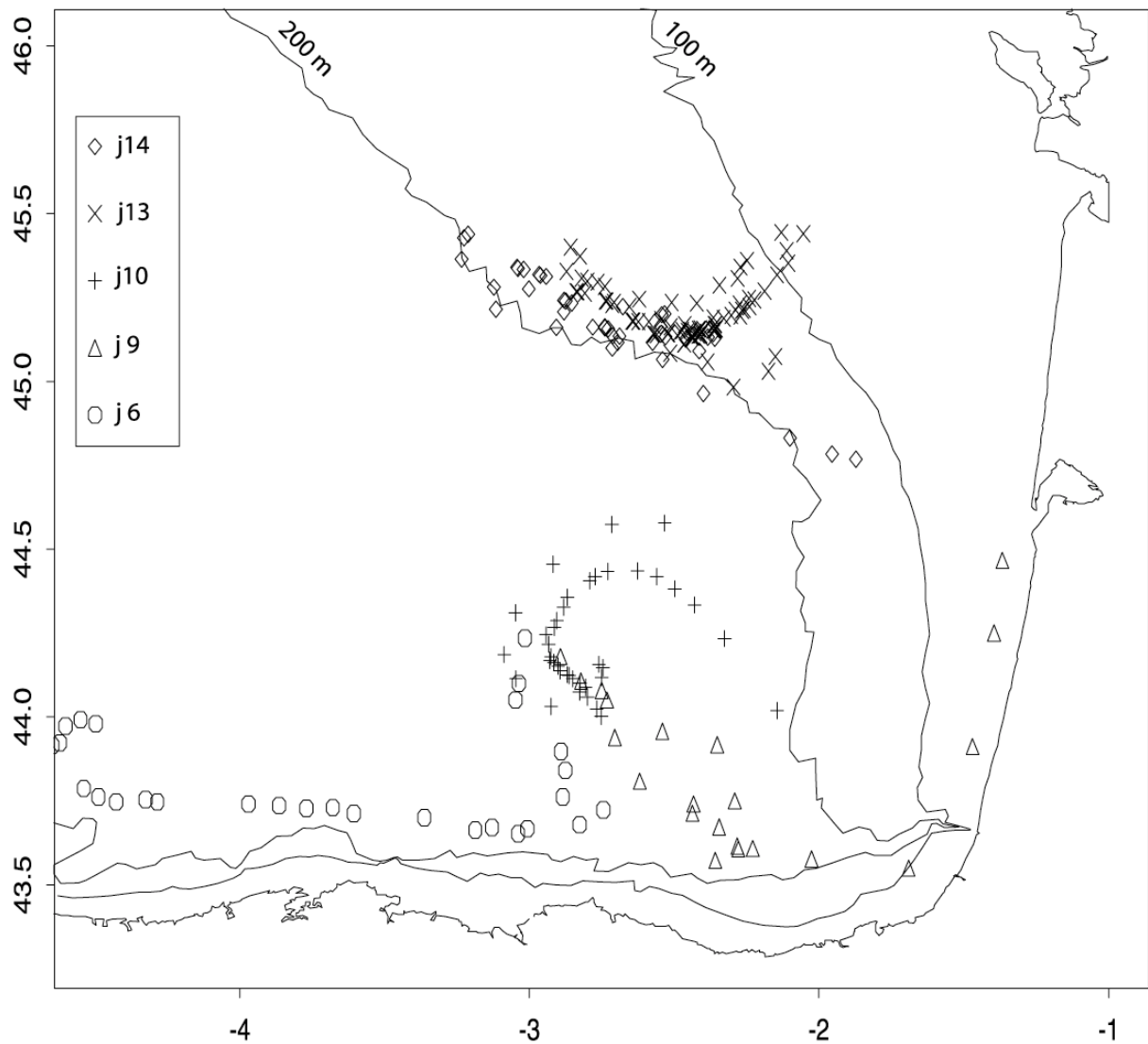


Figure 8 : Potential locations of juveniles every five days between the age of 40 days (after hatching) and the age of sampling, according to the transport model. *j6, j9, j10* : samples of juveniles collected in September 1999 off the Spanish shelf break. *j13, j14* : samples of juveniles collected in September 1999 over the French shelf (see Fig.1).