Coupling the otolith growth history of anchovy larvae
with the physical history of water masses tracked in a hydrodynamic model

by

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Larval growth is one of the major indicators in the field that can be coupled with physical and food chain characteristics in order to understand larval survival and recruitment processes. Anchovy in the bay of Biscay has shown major recruitment variations in the past ten years, varying between 2 and 9 billion individuals. In 1998, an ichtyoplankton survey was performed on anchovy spawning grounds in Biscay. Daily increments in the otoliths of the sampled anchovy larvae were used to determine individual growth curves and hatch dates. Virtual buoys were released in a hydrodynamic model on these hatch dates in order to track water masses until the sampling dates. Then the buoys trajectories ending in the sampling area on the sampling dates were considered as potentially representative of the trajectory and environment experienced by the larvae. An attempt is made to relate the individual growth history of some larvae to the physical history of their associated water masses.

Keywords : bio-physical coupling, recruitment, anchovy, growth, larvae, otolith.

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INTRODUCTION

The coupling of individual larval growth *in situ* and environment in order to better understand fish recruitment processes has been performed both directly, by repeated sampling of a patch of larvae and simultaneous environmental measurements (Gallego et al., 1996, Gallego et al., 1999) and indirectly, using an individually based growth model along particles tracked in a hydrodynamic model (Heath et al., 1997).

An intermediate approach is presented here. It consists in associating sampled larvae with water masses tracked in a hydrodynamic model and potentially representative of the trajectory and environment experienced the larvae. The growth history of the larvae determined by otolith microstructure analysis can then be related to the physical history of the coupled water masses.

Growth and survival are closely related in the early life history of fish (Houde, 1987), the fast-growing individuals having supposedly more chances to survive. In Biscay, anchovy recruitment has varied between 2 and 9 billion individuals in the past 12 years. These variations were well related (75 %) with the variations of meso-scale physical processes estimated from hydrodynamic model simulations (Allain *et al.*, 1999). Therefore relationships between the growth rates of the surviving larvae and the physical parameters recorded along trajectories of associated water masses are looked for. The paper presents the methodology used and preliminary results prior to a statistical modelling.

MATERIALS AND METHODS

Determination of birth dates and growth curves using otolith microstructure analysis

In June 1998, an ichtyoplankton survey was performed over the whole continental shelf in SE Biscay, which is a major spawning ground of anchovy *Engraulis encrasicolus*. Larvae were sampled with towed hauls at 2 knots of the "Carré Net" (Bourriau, 1991) mounted with a 315 μm mesh. Anchovy larvae concentrations were found off the Gironde estuary and in an area above the shelf break (Fer à Cheval), cf. Fig. 1. 10 hauls were performed in both areas. 67 larvae sampled in the Gironde area and 37 larvae sampled in the Fer a Cheval area were analyzed.

The age of each larvae 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 sampled anchovy larvae were 15 to 29 days old (after hatching). Date of hatch was then deduced from the age estimated and the date of sampling. Otolith width was also measured every five increments from the inner-most increment to the edge of the otolith. Otolith growth was adopted as a proxy measurement for somatic growth (Garcia *et al.*, 1998). The growth curves obtained were both plotted against age (Fig. 2) and date (Fig. 5).

Selection of water masses trajectories tracked in a 3D hydrodynamic model

A 3D model of the French Atlantic shelf has been developed at IFREMER to study the shelf hydrodynamics and the evolution of hydrology (Jégou and Lazure, 1995). 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 Loire and Gironde rivers.

The simulation domain corresponds to the French continental shelf of Biscay (Fig. 1). It extends from the French coast to approximately the 200 m isobath and from the English Channel entrance (49°N) to the Gouf de Capbreton (43°50'). The numerical grid has a 5 km x 5 km mesh on the horizontal plane and 10 levels on the vertical. The time step is approximately 900 seconds corresponding to a fixed portion of the tidal cycle. The temperature and salinity fields calculated by the model have been validated by comparison with survey data and with satellite observations (Jégou and Lazure, 1995).

Anchovy larvae 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. We defined a water mass as the upper 30 m water column at a given location. Average physical parameters over this water mass were estimated every hour using the hydrodynamic model : the three components of velocity, temperature, salinity, a stratification index and a turbulence index (diffusivity coefficient Kz). 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 from each point of the model grid (5 km x 5 km) every two days during the hatching period of the sampled larvae (Fig. 3). The buoys trajectories were stopped on the sampling dates. Then the trajectories ending in the larvae sampling area on sampling dates were selected.

Every trajectory beginning on the day of hatch of a given larva and ending in the sampling area on the day this larva was fished represents a trajectory potentially experienced by the larva during its early life. The "physical history" recorded along these selected trajectories reports the environmental conditions possibly experienced by the larva. The starting locations of these selected trajectories correspond to the potential hatching area of this larva.

Analysis of the influence of physical events on larval growth prior to growth modelling

Each individual otolith growth curve can be viewed as a realization of the growth process under a special spatio-temporal series of environmental events recorded along the associated water mass trajectory. Therefore the couples (larval growth history, water mass physical history) represent an interesting material for studying the *in situ* relationships between larval growth and environment, in order to set thresholds on physical variables and/or define categorical states (good or bad) of the larval environment.

Because of the difference between the hydrodynamic model scale and the scale relevant to larvae, a single trajectory cannot realistically be coupled with a given larvae. The trajectory selection procedure implies that all the larvae of the same age and sampled in the same area will be associated with the same set of selected trajectories. Therefore stochastic modelling is necessary to account for the growth variability in a given set of larvae and the physical variability in the set of trajectories associated with it (cf. Mahévas *et al.*, 2000). An exploratory analysis of the biological and physical data is required first in order to build modelling hypotheses. Here we looked for special features in growth and physical data and the possible links between them.

The otolith growth rate of an individual on day t depends not solely on its surrounding environment but also on its past growth history and other individual characteristics such as egg size or quality (Heath and Gallego, 1997). Therefore it is necessary to distinguish growth variability due to the environment from growth variability due to individual factors. A similar and simultaneous trend observed in a significant number of individual otolith growth curves must be the mark of an environmental influence. Then we looked for such common trends in the individual growth data. A typology of the growth curves of the larvae sampled in the Gironde area has been performed in this objective.

In recruitment process, the survivors correspond supposedly to the fast-growing individuals. Therefore a low growth rate or prolonged decrease in growth rate must lead to larval mortality. So a simultaneous decrease in the growth rates of a set of larvae must be associated with environmental conditions detrimental to them. On the opposite, a common increase in the growth rates of a set of larvae could help us to characterize optimal environmental conditions for growth. Therefore we looked for such features in the individual growth data.

PRELIMINARY RESULTS

The physical data sets have been only partially investigated so far. Therefore only a few observations can be reported at this stage.

Differences in growth and physical environment between the two sampling areas

The larvae samples from the two sampling areas (which are 50 km apart) showed two distinct otolith growth patterns (Fig. 2) : mean daily growth rates were on average 60 % higher in the Gironde area than in the Fer à Cheval area (cf. Table 1). It is also noticeable that no value lower than 0.7 µm/day was recorded, while values between 0.8 and 1 µm/day were frequent in the Fer a Cheval sample.

The hydrodynamic model simulations show that the particles associated with the Gironde larvae remained from hatch dates to sampling dates within a lens of stratified/low salinity/warm water (Gironde river plume) surrounded by a circular haline circulation and moving slowly southwards (Fig. 4). These very specific conditions seem to have supported high larval growth rates.

On the opposite, the Fer a Cheval larvae did not experience any similar hydrological structure and travelled in more saline oceanic waters over or beyond the continental shelf. This area stands at the edge of the hydrodynamic model extent. No further bio-physical coupling has been made for this area for the moment.

Growth rate decreases in the Gironde sample and physical events along trajectories

We made a simple typology of the 67 individual otoliths growth curves of the Gironde sampled larvae. A majority of the larvae (55) showed an almost continuous exponential increase of the absolute otolith growth rate for the entire period. Among the other larvae, two sets of individuals showed simultaneous growth rate decreases (Fig. 5) : one during the 3-9 June period (4 individuals) and the other one during the 10-13 June period (6 individuals).

A quarter of the trajectories associated with the first set of larvae show a temporary decrease in stratification and temperature and increase in salinity from 27 May to 3 June (cf. Fig. 6). All the trajectories examined show a peak of wind-induced turbulence (up to 15 m.s^{-1}) from 11 to 13 June, which may be related to the growth decrease of the second set of larvae. A complete statistical analysis is needed to confirm the idea of a detrimental effect of the recorded physical events on larvae.

CONCLUSION

The paper presents the methodology and preliminary analysis required for the coupling of growth trajectories of larvae with the spatio-temporal characteristics of water masses tracked in a hydrodynamic model. In the future stochastic modelling, individual larval growth will be studied as a function of past otolith growth and environmental factors at different time steps. The accuracy of this coupling will mainly depend on the quality of the information derived from otolith microstructure, the difference between larval and hydrodynamic model scales and the nature of the links between growth rate and survival in fish early life stages.

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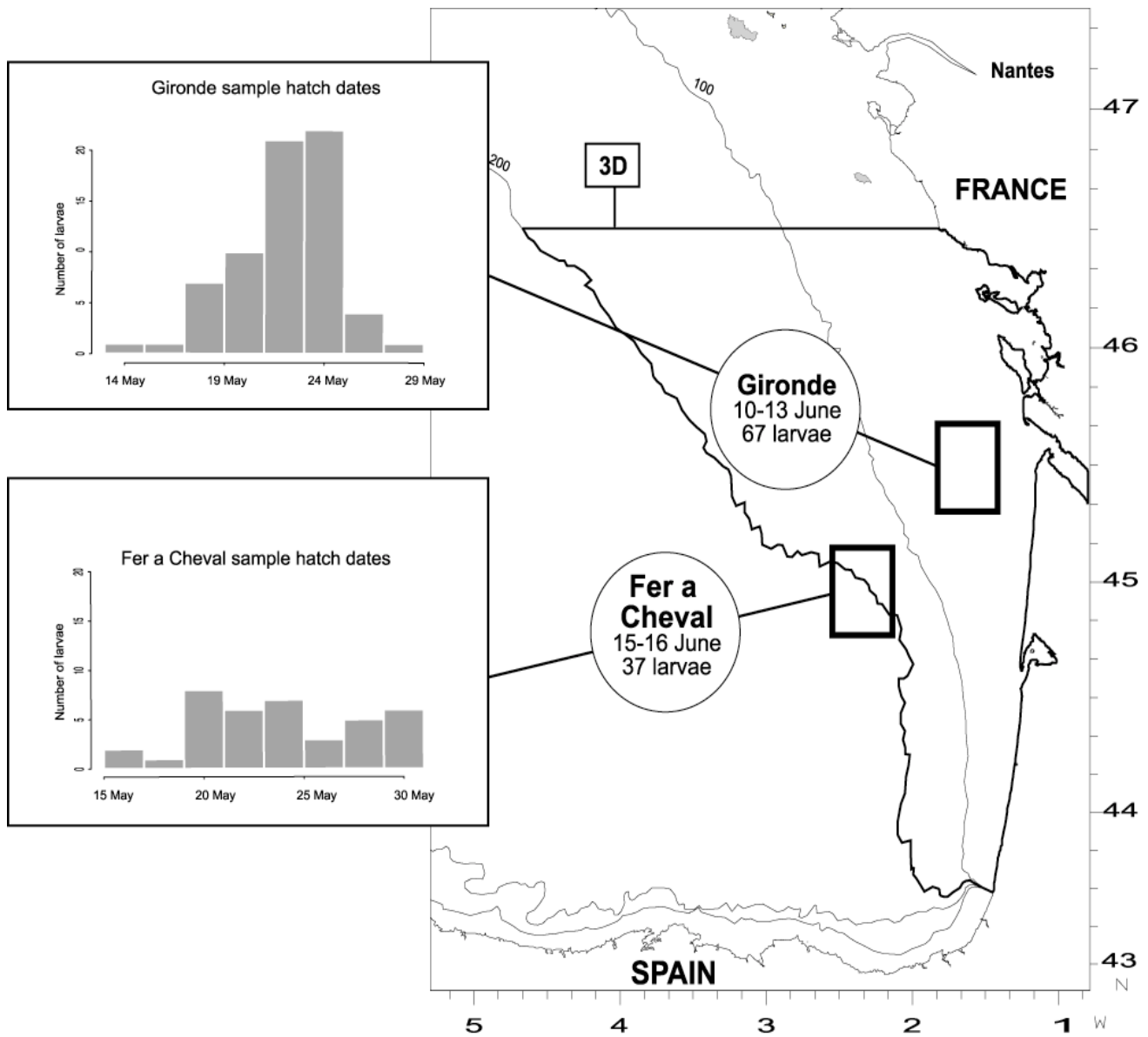
Figure 1 : Synoptic description of the anchovy larvae sampling surveys in June 1998 in the Bay of Biscay. Sampling areas, sampling dates and hatch dates of the larvae are illustrated. 3D = hydrodynamic model domain.
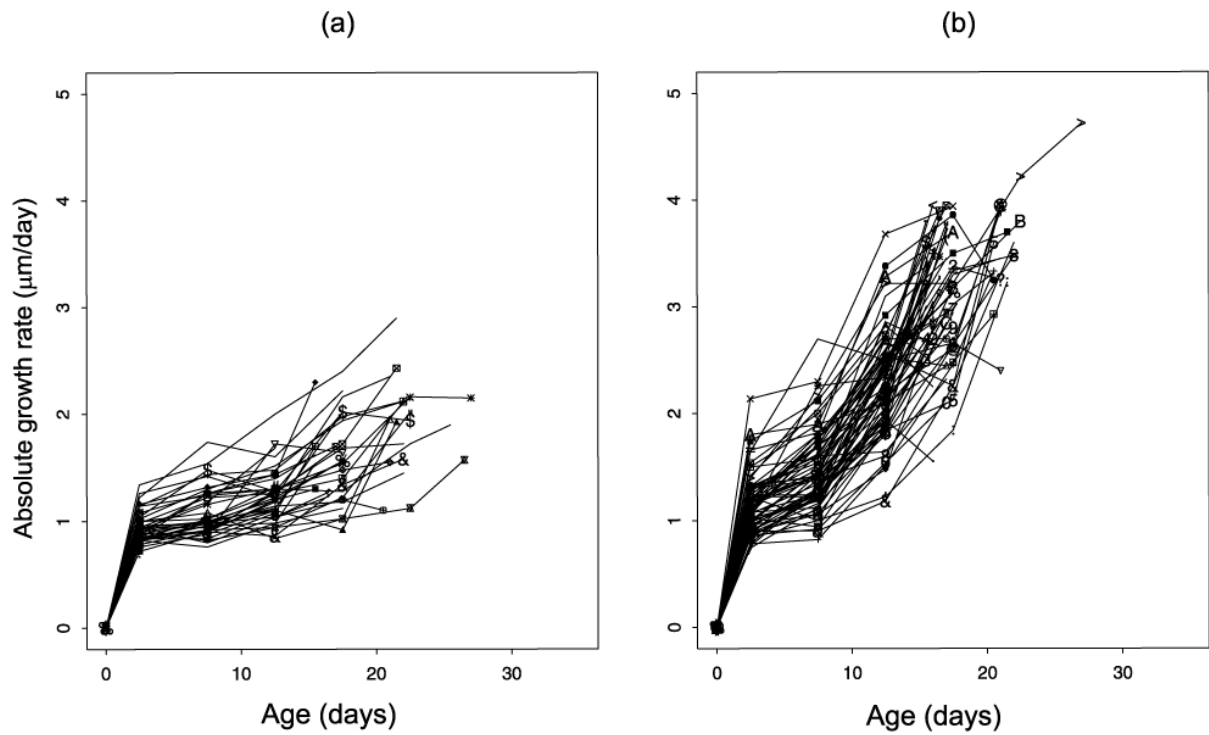
(a)   (b)

Figure 2 : Absolute otolith growth curves (μm/day) of anchovy larvae sampled in (a) Fer a Cheval and (b) Gironde areas.

Mean daily otolith growth rate (μm/day)	Total average	Min.	Max.
Gironde area	1.99	1.32	3.33
Fer a cheval area	1.26	0.89	2.12

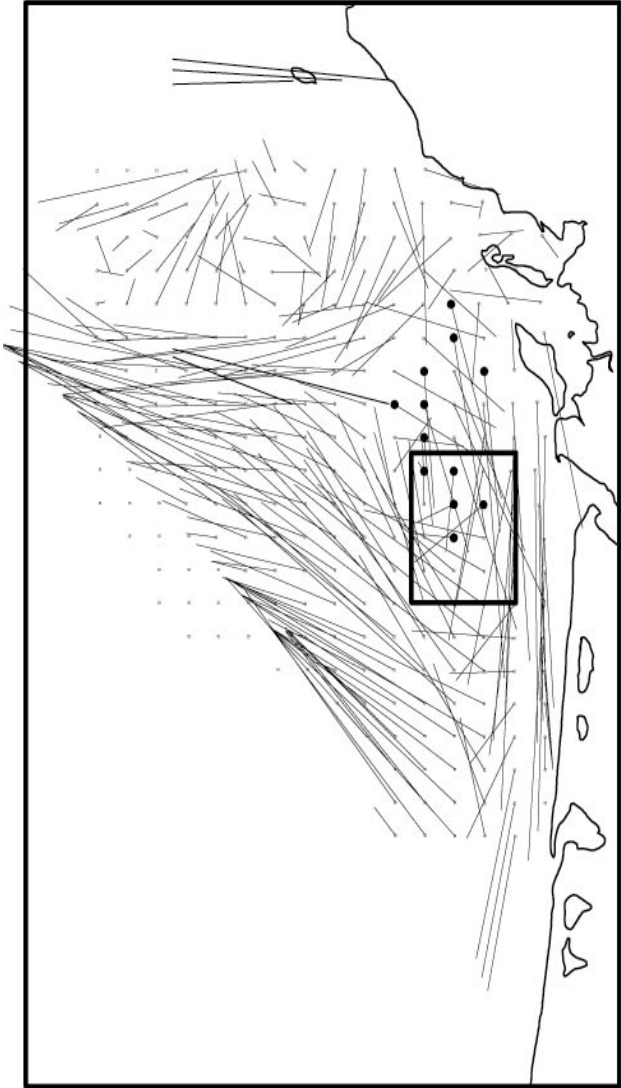Table 1. Growth characteristics of anchovy larvae sampled in the Gironde and Fer a Cheval areas in June 1998.

Figure 3 : Release (on 15/5/98) and arrival (on 13/6/98) locations of a set of water masses tracked in the hydrodynamic model. The water masses found in the Gironde sampling area
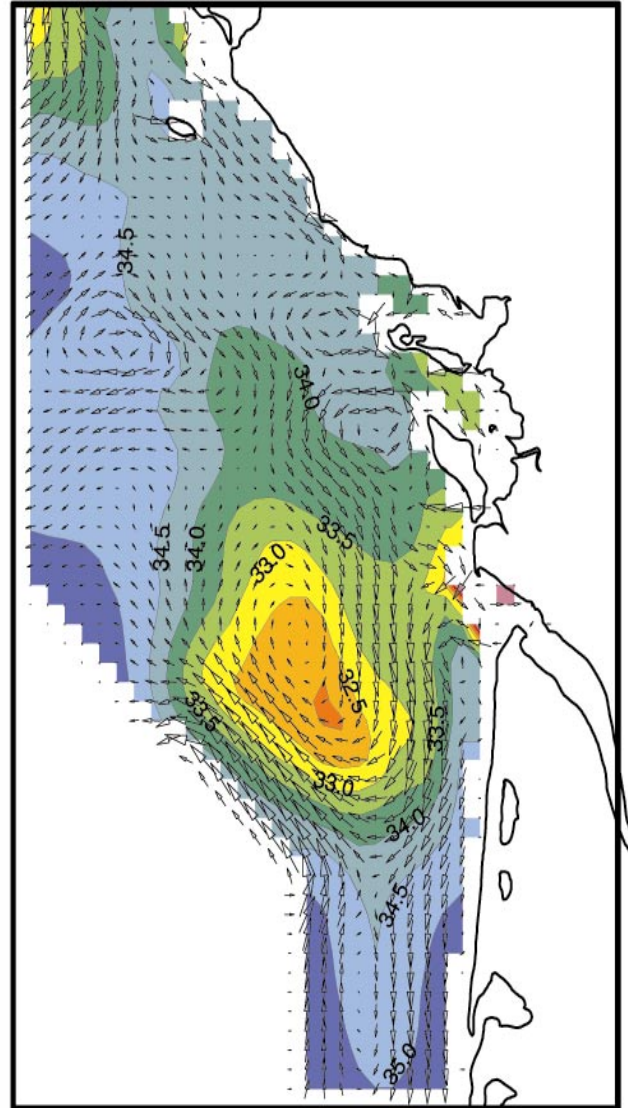

Figure 4 : Salinity and currents at 10 m depth on 30/5/98 estimated by the hydrodynamic model, showing a low salinity water lens (Gironde river plume) with surrounding haline
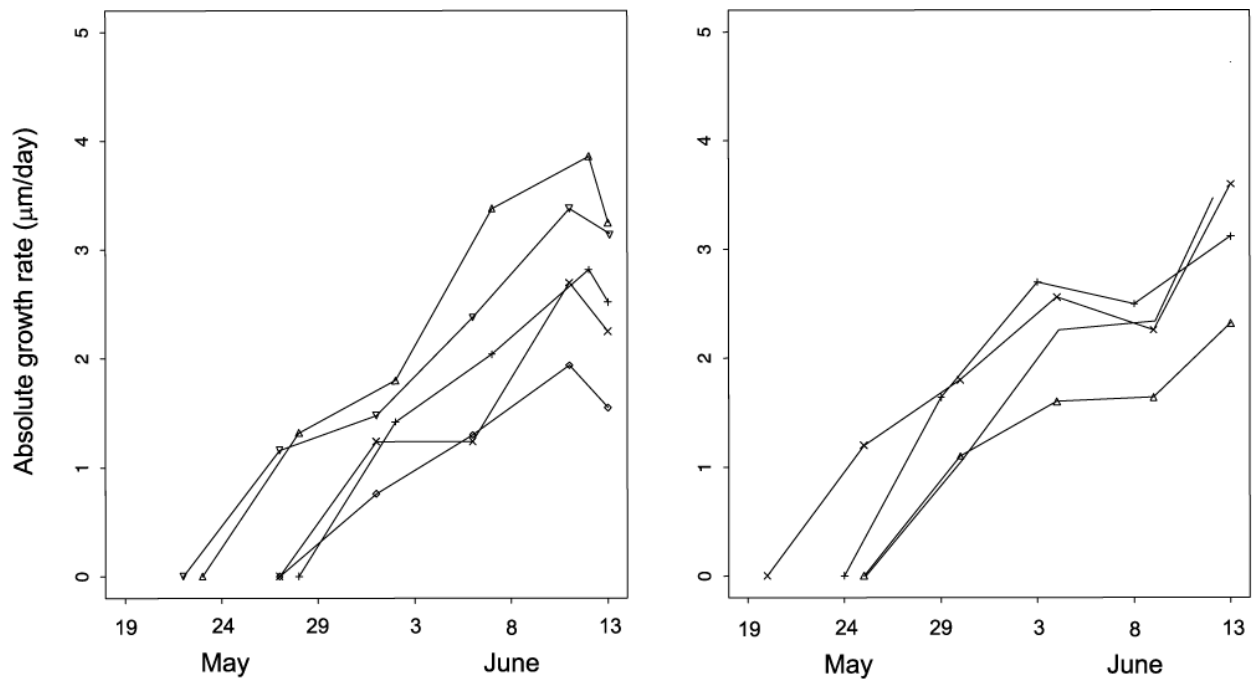
Figure 5 : Individual otolith growth rate of some anchovy larvae sampled in the Gironde area in June 1998. Set of larvae (a) curves show a simultaneous decrease after 10 June while set of larvae (b) curves show a simultaneous and temporary decrease between 3 and 8 June. These decreases may be indicative of environmentally-induced growth variability.
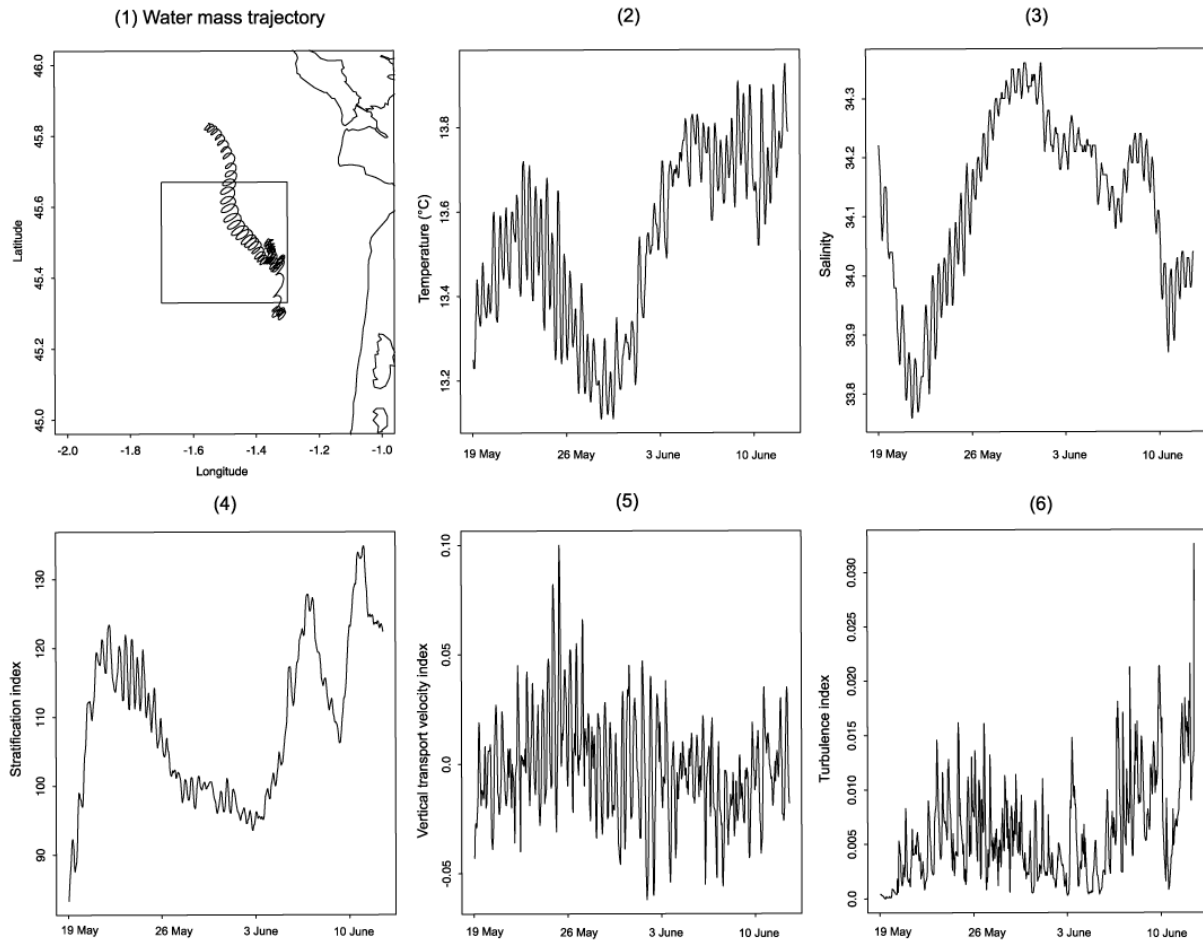
Figure 6 : An example of hydrodynamic model output for a water mass coupled with larvae of set (b) of Fig. 5. (1) Water mass trajectory from 17 May to 13 June. Hourly records of (2) temperature, (3) salinity, (4) stratification index, (5) vertical transport velocity index, (6) turbulence, averaged over the surface 30 meters. A decrease in temperature and stratification and increase in salinity can be observed between 27 May and 3 June.