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A one-dimensional model for the vertical distribution of fish eggs: sensitivity analysis and validation

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Modelling the vertical distribution of fish eggs results of prior importance when monitoring fish population reproductive potential in the context of conservation plans from fast underway continuous samplers, as well as for adequate sampling when assessing fish stocks with egg production methods. Fish eggs being passive particles, their vertical distribution is determined by a few parameters amongst which density, dimension, wind and tidal induced turbulence, and vertical hydrological structure. A one-dimensional vertical bio-physical numerical model was developed which was adapted to the hydrology of shelf seas under the influence of tidal currents, wind induced circulation and river discharges. The biological part of the model parameterised the ascent velocity of the egg as a function of egg properties (dimension, density) and water properties (density, viscosity, turbulence). Being dynamic, the model had a turbulence closure achieved by a k-l scheme. The model parameters were the surface wind, the tidal current, the T-S profile and the egg diameter and density which were kept constant in time. The model had the capacity to generate sub-surface egg maxima in particular conditions, e.g., in areas under the influence of river plumes, as well as homogenise the egg distribution under wind and tide forcing. Sensitivity tests were carried out to study the response of the model to variations in the model parameters, for a variety of hydrological conditions. The modelled egg vertical distributions were validated by comparison of the model results with egg distributions sampled in the field. The analysis highlighted variability in fish egg density of anchovy sardine and sprat across years and stations with a potential link between egg density and surface sea water density. The validated model is a tool for the analysis of shelf seas fish egg vertical distributions.

Key words: Bio-physical coupling, Fish egg buyoancy, Vertical distribution, CUFES

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1. Introduction

The vertical distribution of fish eggs and larvae is a central knowledge in fisheries science, being related to recruitment understanding, stock monitoring and ichtyoplankton sampling. The vertical distribution of eggs and larvae is essential for understanding the impact on stock recruitment of the ichtyoplankton's (i) horizontal drift (e.g., Heath et al., 1991; Stenevik et al., 2001; Parada et al., 2003), (ii) food availability (e.g., Palomera et al., 1991; Conway et al., 1997) and (iii) survival habitats (e.g., Nissling and Vallin, 1996). It is also of prior importance for estimating egg ambient developmental temperature when evaluating fish stocks using egg surveys (e.g., Zeldis et al., 1995; Motos and Coombs, 2000; Coombs et al., 2001). Last it garantees efficient quantitative sampling of the ichtyoplankton at sea (e.g., Moser and Pommeranz, 1999). Modelling the vertical distribution of fish eggs has been recently revived (Boyra et al., 2003) because of the development of the egg pump CUFES (continuous underway fish egg sampler, Checkley et al., 1997) operating at 3m depth and its potential use in egg surveys for adult stock evaluation (Checkley at al., 2000; Lo et al., 2001) as well as its potential coupling with acoustics recording the adult spawning fish (Petitgas et al., 2002).

The vertical distribution of pelagic eggs is determined by a set of interacting biological and physical processes (Sundby, 1991), namely the properties of the eggs (density, dimension) and the ambient sea water (density, viscosity, turbulence). Two models for predicting the egg vertical distribution have been developed (Sundby, 1983; Westgard, 1989). Sundby (1983) proposed for an homogeneous wind mixed layer, an analytic steady-state solution which balances the egg ascent velocity with the wind induced turbulence. Westgard (1989) proposed a dynamic numerical modelling with a two level turbulence closure scheme to account for depth varying turbulent diffusion. This approach allowed to analyse transient egg distributions through time as well as steady-state distributions. The model of Sundby (1983) was successfully applied in outer ocean areas where the hypotheses of homogeneous turbulent diffusion in the mixed layer was relevant (Sundby, 1983; Adlandsvisk et al., 2001; Stenevik et al., 2001). This assumption was relaxed to account for given parametric formulations of depth varying turbulence in order to model sub-surface peaks in the egg distribution but with mitigating success (Tanaka, 1992; Boyra et al., 2003). In contrast the numerical model of Westgard (1989) takes in charge a variety of hydrodynamic conditions and in particular when haline stratification of the water column generates complex depth variation in turbulent diffusion.

On the French shelf in the bay of Biscay, pelagic fish stocks and pelagic ecosystem are monitored by spring-time fisheries acoustic surveys, with particular focus on anchovy and sardine. During the surveys the CUFES egg pump is operated together with the acoustics allowing for the cross-validation of assessment methods and the study of the ecology of spawning grounds. For these purposes the pumped 3m depth egg concentration needs to be converted to a vertically integrated egg abundance.

Such conversion requires modelling the egg vertical distribution. During spring-time, hydrological conditions are diverse on the French Biscay shelf (as observed in the series of surveys) with water column stratification being due to salinity or temperature or both and with turbulent diffusion being due to wind and tide (Planque et al., 2003).

The object of the present paper was to develop further the numerical model of Westgard (1989) to incorporate tidal forcing and achieve a modelling tool of vertical egg distributions for shelf seas including areas under the influence of tide and river plumes. The model sensitivity to input parameters (wind, tide, egg density and diameter) was analysed in a variety of hydrological situation typical of Biscay French shelf. The model was then validated by comparing its outputs with published in situ vertical distributions selected from the literature. It appeared that egg density could vary from year to year depending on surface hydrological conditions.

2. Materials and methods

2.1 The one-dimensional vertical model

2.1.1 The physical model

The hydrodynamic model is a one-dimensional dynamical and numerical model forced by wind and tide. In order to simulate tidal effects, free surface elevation gradients are considered. The model has five state variables, namely temperature, salinity, velocities (u,v) and turbulence kinetic energy. The turbulence closure is achieved by an algebric formulation of the mixing length (k-l scheme).

The two components of the velocity:

$$\begin{cases} \dfrac{\partial u}{\partial t} - fv = -g\dfrac{\partial \xi}{\partial x} + \dfrac{\partial}{\partial z}\left(n_z \dfrac{\partial u}{\partial z}\right) & (1) \\ \dfrac{\partial v}{\partial t} + fu = -g\dfrac{\partial \xi}{\partial y} + \dfrac{\partial}{\partial z}\left(n_z \dfrac{\partial v}{\partial z}\right) & (2) \end{cases}$$

with the following notations:

t:time

z : vertical coordinate (positive upward)

u(z,t) : E-W velocity (m s^{-1})

v(z,t) : N-S velocity (m s^{-1})

g: gravitational acceleration (9.81 m s^{-2})

f: Coriolis parameter (10^{-4} s^{-1})

$n_z(z,t)$: vertical eddy viscosity (m^2 s^{-1})

$\left(\frac{\partial \xi}{\partial x}, \frac{\partial \xi}{\partial y}\right)$: free surface elevation gradient

The surface condition:

$$n_z\left(\frac{\partial u}{\partial z}, \frac{\partial v}{\partial z}\right) = \left(\frac{\tau_x}{\rho}, \frac{\tau_y}{\rho}\right)$$

with the following notations:

$\left(\frac{\tau_x}{\rho}, \frac{\tau_y}{\rho}\right)$: surface wind stress components

$\rho(z)$: density of sea water (kg m^{-3})

The bottom condition:

$$n_z\left(\frac{\partial u}{\partial z}, \frac{\partial v}{\partial z}\right) = C_d \sqrt{u_b{}^2 + v_b{}^2}\,(u_b, v_b)$$

where C_d is the drag coefficient (2,5 10^{-3} SI) and u_b,v_b the velocities in the bottom layer.

The tidal forcing:

The linear theory of tide indicates that the horizontal gradient induced by a tidal wave propagating in one direction can be expressed as the following horizontal gradient:

$$\left(\frac{\partial \xi}{\partial x}, \frac{\partial \xi}{\partial y}\right) = \frac{gU_0}{cT}\left(\cos(2\pi t/T), \sin(2\pi t/T)\right)$$

with the following notations:

T: M_2 tidal period (44712s)

U_0: the maximum of tidal current reached during a tidal cycle

$c = \sqrt{gH}$: the velocity of tidal wave (H being the water depth)

The turbulence closure scheme:

The turbulence closure model is based on the turbulence kinetic energy (TKE) state equation and an algebric formulation of the mixing length (Luyten et al, 1996):

$$\frac{\partial k}{\partial t} = \frac{\partial}{\partial z}\left(n_z \frac{\partial k}{\partial z}\right) + P_s + G - \varepsilon$$

with the following notations:

$k(z,t)$:TKE (m^{-2} s^{-2})

ε: dissipation rate of TKE (m^{-1} s^{-3})

Ps: production of TKE by vertical velocity gradient: $P_s = n_z\left(\left(\frac{\partial u}{\partial z}\right)^2 + \left(\frac{\partial v}{\partial z}\right)^2\right)$

G: reduction of TKE by vertical density gradient: $G = -gk_z \frac{1}{\rho}\frac{\partial \rho}{\partial z}$ with k_z the eddy diffusivity

In the present one-equation turbulence closure scheme, ε is given by a function of TKE and the mixing length *l*:

$\varepsilon = \varepsilon_0 \frac{k^{3/2}}{l}$, where ε_0 =0.166 and $l(z) = \kappa z(1 - z/H)^{1/2}$ with the Karman constant $\kappa = 0.4$

Finally, turbulent eddy viscosity and eddy diffusivity are given by:

$n_z = S_u k^2/\varepsilon$ and $k_z = S_b k^2/\varepsilon$

Where S_u and S_b are stability functions which expressions can be found in Luyten et al. (1996).

Though similar to that of Westgard (1989), our model differs from it in two ways. In our model, (i) tidal current is taken into account (which was not the case in Westgard, 1989) and (ii) ε is estimated as a function of the mixing length (we have a k-l closure and not a k-ε closure as in Westgard, 1989). Luyten et al. (1996) compared different turbulence closure schemes for shelf stratified waters and concluded that there was no difference in the results between the two schemes, the k-l closure scheme being less computer intensive.

Being dynamical and numerical, the model can deal with homogeneous or stratified vertical profiles of temperature and salinity and in particular it can accommodate any type of gradient in turbulent eddy diffusivity due to complex haloclines on the shelf under the influence of river plumes. The model can also estimate the steady-state vertical distribution as well as a time-dependent distribution depending on the duration of the simulation in relation with that of the egg stages.

2.1.2 The coupled biological model

The hydrodynamic model is coupled with a biological model which parameterises the ascent velocity of fish eggs. The state equation of the egg concentration is:

$$\frac{\partial \varphi}{\partial t} = \frac{\partial}{\partial z}\left(k_z \frac{\partial \varphi}{\partial z}\right) - \frac{\partial w\varphi}{\partial z} \quad (3)$$

where φ is the egg concentration (nb eggs m^{-3}), w the egg ascent terminal velocity (m s^{-1}), k_z the eddy diffusivity (m^2 s^{-1}). The vertical egg distribution φ thus results from the interaction between turbulent mixing as given by k_z and advection as given by w, where k_z and w are estimated by the physical and the biological parts of the model.

The ascent velocity w depends on the egg diameter d, the density difference $\Delta\rho$ (kg m^{-3}) between the egg and the ambient sea water and the viscosity μ of the sea water. The parameterisation of w is given by Stokes's law or Dalavalle's law depending on the value of the Reynolds number (Dallavalle, 1948; Hutchinson, 1967; Sundby, 1983). The switch to Dalavalle's parametrisation from Stocke's law with increasing Reynolds number has the consequence to lower the ascent velocity of the egg when sea water becomes less viscous and more turbulent. When the Reynolds number $Re = \rho_{water}\, w\, d \,/\, \mu$ is smaller than 0.5, viscosity forces dominate over frictional forces and w is given by Stockes's law:

$$w = \frac{g\, d^2\, \Delta\rho}{18\,\mu}$$

where μ is the dynamic viscosity (kg m^{-1} s^{-1}) which depends on temperature and salinity (Table 1). When the Reynolds number is greater than 0.5, viscosity forces decrease in importance because of an increase in turbulence and in that case w is given by the equation of Dalavalle (1948):

$$w = \frac{K_I\, d_o\, \Delta\rho^{2/3}}{\mu^{1/3}}$$

where K_I is a constant equal to 19 in c.g.s. units (Sundby, 1983) and d_o is given by (Sundby, 1983):

$$do = d - c\, D = d - c\left(\frac{9\,\mu^2}{\rho_{egg}\, g\, \Delta\rho}\right)^{1/3}$$

with D is the uppermost limit of egg size to which the Stokes equation applies and c a constant equal to 0.4 for spheres.

2.1.3 Model implementation

Model resolution

Equations 1 and 2 are discretized on the vertical on a staggered grid: n_z, k_z are calculated between the points at which are calculted u, v and φ. Equations 1 and 2 are not solved at the same time but alternatively every half time step to obtain a temporally centered scheme for the Coriolis force. Variables φ, TKE, n_z and k_z are calculated every time step. All vertical derivatives are considered as implicit which leads to a classical three diagonal matrix solved by standard method.

Model application

The vertical grid mesh size was 1 m. The maximum tidal velocity, U_0, varies in space and was set as a local condition like e.g., Coriolis parameter, f, and water depth, H. Values of U_0 for the Bay of Biscay and English Channel are calculated by a general 2D tidal model, which gives similar results than earlier calculations of Pingree et al. (1982) and Le Cann (1990). Sea water density profile (derived from the vertical temperature and salinity profiles), wind speed, tidal current U_0, egg diameter and density were kept constant during the whole simulation.

Characteristic time and initial condition

The steady-state egg distribution was obtained by the balance between turbulent mixing and advection as formulated in equation (3). The characteristic time was derived from the dimension analysis of equation (3). The egg migration time scale, namely $H/\overline{w}$, is the time necessary for the egg to attain a steady-state distribution starting from a homogeneous initial egg distribution by advection only. The physical mixing time scale, namely H^2/k_z, is the time necessary to attain a steady-state by vertical mixing only. The relevant characteristic time is the smallest of these two time scale, telling if the steady-state is attained because of physical mixing or egg migration. If the characteristic time is smaller than the egg stages duration, the egg can attain its steady-state distribution. The in situ distribution is then independent of the initial condition and can be estimated with the steady-state solution of the model. In contrast, if the characteristic time is greater than the egg stages duration, the egg cannot attain a steady-state. In that case, the in situ egg distribution will depend on the initial condition of spawning and can only be estimated by a transient solution of the model. All simulations were performed for 20 days starting from a homogeneous vertical distribution, which was a sufficiently long time for the model to attain a steady-state in all the considered cases. The characteristic time was estimated at the beginning of the simulation.

2.2 Model sensitivity

Sensitivity of model outputs to variations in the physical and biological input parameters was analysed for typical spring-time bay of Biscay hydrological situations and for anchovy and sardine. Four input parameters were retained: wind, tide, egg diameter and egg density.

Spring-time (may-june) fisheries acoustic surveys of IFREMER provided temperature and salinity profiles at CTD stations covering the entire French shelf of the bay of Biscay (2000-2003). The hydrological profiles where characterised using four variables following Planque et al. (2003): surface temperature and salinity, bottom temperature, depth of maximum density gradient. A hierarchical clustering of all CTD stations was performed. Four hydrological groups were identified: group G1 was characterised by a small density gradient, group G2 by a haline gradient, group G3 by a temperature gradient and group G4 by both haline and temperature gradients (Table 2, Fig. 1). In each group, the station closest to the group centre was selected to represent the group. These stations were used as reference stations in the sensitivity analysis with their hydrological structure, wind and tide conditions.

A reference run (RR) was performed at each reference station using the parameters compiled in Tables 2 and 3: observed wind at reference station, tidal current of 0.8 m s^{-1} corresponding to an average value for Biscay, the Celtic Sea and the English Channel, average egg diameter and density reported by Coombs et al. (in press) and Boyra et al. (2003). Then each parameter (wind, tide, egg diameter and density) was varied one at a time, the other parameters being kept at their reference value. For each run and each hydrological condition, the root mean square difference (RMSD) between the estimated egg distribution and that of the RR was computed over the first 50 m. The egg concentration φ was expressed as the percentage at depth of total egg abundance in the water column. RMDS values allowed to quantify the impact on the egg distribution of each input parameter in each hydrological condition, compare the impact between parameters in each hydrological condition and compare the impact for each parameter accross the hydrological conditions. Also focus was put on the first 5 m of the vertical distribution using another parameter than the RMSD: the percent increase or decrease of eggs in the first 5 m relatively to the egg abundance of the RR in those first 5 m.

2.3 Model validation

The model was validated using published in situ egg vertical distributions sampled with the Longhurst-Hardy Plankton Recorder (LHPR, Williams et al., 1983). At each of the LHPR sampling stations, the following parameters were necessary to run the model: geographical position and date, temperature and salinity profiles, wind speed, tidal current, egg diameter and density. Published material was selected based on the availability of this set of parameters in the articles as well as on the processes to be validated. The biological part of the model was validated using deep egg distributions of blue whiting that were below the depth of wind induced turbulence (Adlansvik et al., 2001). The model dynamics in the presence of wind and tide was validated using egg distributions of sardine and sprat in the Channel in summer with thermal stratification as well as in autumn with homogeneous water column structure (Coombs et al., 1985). The model dynamics in the presence of wind, tide, thermal and haline stratifications was validated using egg distributions of anchovy and sardine in Biscay in spring (Motos et Coombs, 2000; Coombs et al., in press). Stations were selected that showed a surface peak, a sub-surface peak and a deep peak in the egg distribution. T-S and egg profiles were scanned from the published figures and interpolated at 1 m interval for comparison with the vertical model output. Egg density was adjusted for the model to best fit the sampled distributions. The adjusted egg density was then compared to available published measurements performed with the density-gradient column of Coombs (1981). In each validation experiment, the egg characteristic time was estimated. Except for the blue whiting for which initial conditions were provided, in all other cases the model initial egg distribution was homogeneous: at each depth, the egg concentration was equal to the total number of eggs counted from bottom to surface at the station divided by depth (grid mesh size being 1 m). The homogeneous initial distribution was equivalent to making no assumption on spawning depth.

3. Results

3.1 Sensitivity analysis

Impact of anchovy egg shape

The egg of sardine is spherical but the egg of anchovy is a prolate ellipsoid. As Stocke's law applies for spheres, the anchovy egg ascent velocity may depart from that calculated with Stocke's law. Hutchinson (1967, Fig.75 p.262) provides corrections from Stocke's law for an ellipsoid as a function of the ratio between ellipsoid axes and the orientation of the ellipsoid during its motion. Coombs et al. (in press) report that the mean egg diameter for anchovy in Biscay was 0.7 mm x 1.5 mm (the sphere of equivalent volume having a diameter of 0.89 mm) and that the orientation of anchovy eggs was along their long axis during measurements in the density-gradient column (the embryo effectively develops at one pole of the egg). In this situation, the ascending velocity of the egg would be 0.96 that of its equivalent sphere (Hutchinson, 1967). This small correction on the egg velocity had no impact on the egg distribution. Anchovy eggs were considered as spheres of equivalent volume, an approach followed by Coombs et al. (in press) for anchovy and Adlandsvik et al. (2001) for blue whiting larvae.

Sensitivity in the first 50 m

From the structure of the model, it is expected that increasing wind will increase mixing from the surface downwards the water column, that increasing tide will increase mixing from the bottom upwards, both resulting in homogenising the egg distribution. Increasing egg size is expected to increase ascent egg velocity and reduce the time scale to attain steady-state. In contrast, increasing egg density is less easily predictable as its effect depends on the sea water density profile. Variation in the input parameters for the sensitivity analysis is compiled in Table 3. The RMSD values (Table 4) showed wind to have an important impact in all hydrological groups and in particular, low wind condition changed radically the egg distribution in group G4. Tide had no effect except in coastal group G2. It is then expected that in coastal waters the spring-neap tidal cycle has a significant effect on the vertical egg distribution. Egg diameter had no impact in groups G1 and G3 but a small one in groups G2 and G4 for both anchovy and sardine. Impact of egg density was similar except that it was very important in groups G2 and G4.

Situations whith high RMSD values were analysed further by examining the egg vertical profiles (Figs 2-5). Low wind condition at station G4 (Fig. 2) allowed the anchovy eggs to concentrate in a pronounced sub-surface peak (8 m depth). The peak was present in the RR but smoothed in the stronger wind condition. Low tidal current at station G2 (Fig. 3) allowed anchovy eggs to concentrate at the surface (0-5 m) which bigger tidal currents did not allow. Increasing anchovy egg density at station G2 (Fig. 4) generated a deep peak (13 m). In contrast, with lower density values the maximum egg concentration was in the surface layer (0-5 m). Increasing sardine egg density at station G2 (Fig. 5) also generated deep peaks (7 m and 13 m). Similarly, with lower density values the maximum was in the surface layer (0-5 m). Similar effects but less pronounced (not shown) occurred at station G4 for both anchovy and sardine. Sardine and anchovy egg profiles were more sentitive to variations in the egg density in the case of complex hydrological structures such as G2 and G4 (typical of the shelf) in comparison to conditions G1 and G3 (more typical of oceanic conditions).

These results show the importance of modelling tide induced mixing, knowing egg density as well as using a dynamic numerical modelling to deal with complex haline and mixed haline-thermal stratifications which are typical of shelf seas.

Sensitivity in the first 5 m.

The impact of variations in the input parameters was further assessed for the CUFES which is a surface pumping device (at 3 m): we estimated the resulting variation in the surface (0-5 m) egg concentration relatively to that of the RR. High variations in this layer occurred in the cases where RMSD was large but also in more cases (Table 5). Variation in this layer was sensitive in nearly all parameters and hydrological conditions, except for tide in groups G1 and G3, anchovy diameter in group G2 and sardine density in groups G1 and G3. RMSD quantified overall variation in the profile shape (50 values used) when here focus was only on 5 values of egg concentration at the surface. This means that CUFES samples are expected to have a high degree of variability and that a precise estimate of the water column egg integral using the model will require a precise control in the input parameters.

2.2 Model validation

Blue whiting along western european shelf edge: Adlandsvik et al. (2001).

The eggs being spawned at 600m depth well below the depth of wind-induced turbulence, the example provided a validation of the biological part of the model, i.e., the switch between Stocke's law and

Davalle's parametrisation depending on the Reynolds number to estimate the ascent velocity of the egg. The article provided in situ egg distributions as well as egg density measurements with the density-gradient column of Coombs (1981). The egg diameter was 1.08 mm constant during all egg stages. The egg density increased with egg developmental time. The model was run starting from an initial (spawning) condition given in the article (peak at 380-400 m) and transient solutions were estimated for the different egg stages depending on the stages durations reported in the article (Table 6). The model allowed to reproduce well the sampled distributions (Fig. 6) thus cross-validating the parametrisation of the egg vertical velocity as well as the egg density measurements.

Anchovy on the French shelf of the bay of Biscay in spring: Motos and Coombs (2000)

Motos and Coombs (2000) report in situ anchovy egg distributions sampled in 1996 on the Biscay French shelf. When the water column was stratified eggs were confined mainly to the upper layer with a surface peak. In areas under the influence of the river plumes where haline and thermal stratification were present, a sub-surface peak in egg abundance was observed close to the pycnocline. At each station the following information was available: position and date, temperature and salinity profiles and wind speed. Tide was deduced from station position and date. Egg density was not available in the article and was adjusted for the model to best fit the sampled distribution. Egg diameter was not available either and we used the value given by Coombs et al. (in press).

Station 9 (28 may 1996) was selected because it showed important thermal and haline stratification in the hydrology, light wind condition and a sub-surface peak in the egg concentration at the pycnocline at 7 m depth (Table 7, Fig.7). The model allowed to reproduce the sampled distribution (Fig. 7). Station 10 (28 may 1996) was also selected because it had a less pronounced gradient in temperature and salinity, greater wind condition and showed a surface peak in the egg distribution (Table 7, Fig. 7). The model also allowed to reproduce the sampled distribution (Fig. 7). The egg density values derived independently for stations 9 and 10 were in close agreement (Table 7), validating further the model. Depending on the hydrological structure and the egg density, the model was able to reproduce the observed sub-surface or surface peaks in the egg distribution.

Boyra et al. (2003) report anchovy egg density measurements performed in 2001 with the density-gradient column of Coombs (1981) using eggs collected close to the spanish coast. The average value in 2001 was 23.26 (sigma-t) with a standard deviation of 0.63 (sigma-t). It is noteworthy that the 2001 egg density were too low to allow for the adjustment of the egg distributions sampled in 1996. The alternative solution was to derive egg density values for 1996 knowing the sampled egg distributions in 1996 and compare these to the 2001 density value. The egg density was 25.83 (sigma-t) according to our model in 1996, raising the question of potential significant variation in egg density.

Sardine on the French shelf of the bay of Biscay in spring: Coombs et al. (in press)

Coombs et al. (in press) report in situ sardine and anchovy egg distributions sampled in 2000 on the Biscay French shelf. Egg distributions were similar to that observed in 1996 for anchovy. Similarly, at each station the following information was available in the article: position and date, temperature and salinity profiles, egg diameter. Tide was deduced from station position and date. Wind was taken from the lighthouse of Chassiron which was the closest to the sampling stations. Again, egg density was not available in the article and was adjusted for the model to best fit the sampled distribution.

Station 29 (18 may 2000) was selected for sardine eggs because it showed an important thermal and haline stratification in the hydrology, moderate wind condition and a sub-surface peak in the egg concentration at the pycnocline at 7 m depth. Again, the model allowed to reproduce the sampled distribution (Table 8, Fig. 8). The egg density adjusted with the model was 24.5 (sigma-t), a value in agreement with the range of values experimentally measured by Coombs et al. (1985) in 1982 in the Channel (24-27 sigma-t) but significantly greater than that measured by Boyra et al. (2003) in 2001 in southern Biscay (23.4 sigma-t, std.dev 0.44). The question of potential significant variation in egg density is therefore also raised for sardine.

Sardine off Plymouth in summer and autumn: Coombs et al. (1985)

Coombs et al. (1985) report in situ sardine and sprat egg distributions sampled in 1982 off Plymouth in the Channel, together with egg density measurements performed with the density-gradient column of Coombs (1981). At each station the following information was available: position and date, temperature and salinity profiles. The hydrological structure showed a thermal stratification in summer while in autumn the density profile was uniform. Tide was deduced from station position and date. Wind on sampling date was taken from the lighthouse of La Hague which was the closest to the sampling station available to us. The egg diameter was not available in the article and we used the value of 1.64 mm reported in Boyra et al. (2003).

Station 8 (7 July 1982) and sation 11 (6 October 1982) were selected because of the difference in hydological and biological structures. In July in the presence of a thermal stratification, the eggs were confined to the first 15 m with a surface peak while in October the egg distribution was less confined and homogeneous in the first 35 m. The model allowed to reproduce the sampled distributions in both cases (Table 9, Fig. 9). The density values adjusted (25.4 and 25.5 sigma-t) were in the range of values given in the article (24-27 and 22-26 sigma-t), thus validating further the model.

Sprat off Plymouth in spring: Coombs et al. (1985)

Station 4 (9 June 1982) was selected because it showed a thermal stratification and a sub-surface peak in the egg distribution at 20 m depth allowing to validate further the model with different egg parameters than previously. The egg diameter was not available in the article and we used the value of 0.9 mm reported in Russel (1976). Again, the model allowed to reproduce the sampled distribution (Table 10, Fig. 10). The egg density adjusted was 26.5 (sigma-t) which was in the range of experimental values measured in the article (23-26.5 sigma-t), thus validating further the model.

4. Conclusion and discussion

Model structure and validation

Because of the dynamic numerical modelling and the turbulence closure scheme, it was possible to reproduce the mixing conditions of a stratified water column in the presence of complex halocline and/or thermocline, under wind and/or tide induced turbulence. These conditions, regularly encountered in spring in the bay of Biscay French shelf, are typical of shelf seas under tidal and river run-off influences. The model developed here is adapted for such conditions and represents a novel tool for modelling fish egg vertical distributions in shelf seas. The bio-physical coupling through the parametrisation of the egg vertical velocity allowed to reproduce the different types of egg vertical distributions encountered in survey data for different species (sardine, sprat, anchovy and blue-whiting): (i) confinement in the upper layers above the pycnocline with a surface peak or homogeneous distribution in the upper layer; (ii) sub-surface maximum at the pycnocline; (iii) deep maximum below the pycnocline. It is noteworthy that the present dynamic numerical modelling was able to reproduce sub-surface maxima in the egg distribution, a feature that Boyra et al. (2003) had difficulties to reproduce using the analytical model of Sundby (1983). The validation exercise required a list of parameters (sampling position and date, temperature and salinity profiles, wind, egg diameter and density) which were not always collected together with the sampling of vertical distributions. It is advised to consider collecting the full set of information in future studies if in situ vertical distributions are to be fully used for validation purposes.

Model sensitivity

Wind controlled the vertical egg distribution allowing for a sub-surface maximum to occur or homogenising the distribution. Tide was also an important forcing parameter in shallow waters (depth smaller than 50 m), with a capacity to also homogeneise the egg distribution. Model results were sensitive to variations in egg density, determining the vertical position of the egg maximum. The egg concentration in the surface layer (0-5 m) was sensitive to variations in all input parameters, making fine scale monitoring of wind and egg density of prior importance if underway 3 m depth CUFES samples are to be converted to vertically integrated egg abundance using the vertical model. The model could be used as an assessment tool for that purpose.

Model limitation

The model could also be used as a tool to investigate biological processes that are not well controlled at present. With the numercial model now at hand which is adapted to shelf seas processes (tide, wind, haline and thermal stratification), model limitation is thought to reside in biological knowledge more than in the model parametrisation. Individual variability in the egg parameters at each station was not taken into account here. It is potentially feasable to incorporate this variability in the coding but this would require knowledge on the probability distributions of egg diameter and density as well as the correlation between them. It is expected that taking into account the at station individual egg variability would result in smoothing the model steady-state profile without changing its shape. The comparison between the at station individual variability with the spatial and inter-annual variability in the average egg parameters should be the basis for justifying the incorporation of the major source of variability. It is anticipated (see below) that the at station individual variability in egg density is smaller than the spatial and inter-annual variability. Variability in egg parameters at difference scales in not enough monitored, making egg parameter values imprecise and thus the modelled distributions. Another point is the dependence of the egg distribution on the initial spawning distribution. The characteristic time is a parameter that gives insight into the subject. On one occasion only (Table 11: sardine at station 12 on 29 may 1996), was the characteristic time greater than the egg life span (12.26 days). This happened when both egg velocity and mixing were small (small difference between egg and sea water density, low wind and tide conditions). The in situ egg distribution was then expected to be dependent on the initial spawning depth. Sardine at this station was omitted from the present study. The model could serve to explore across a variety of species and hydrological conditions different vertical spawning strategies.

Variation in the egg density

The validation exercise highlighted significant variation in egg density between years, making the use of density measurements problematic when performed in other conditions than that of the sampled vertical distributions. When egg density was measured in the conditions in which the egg distribution was sampled, e.g., blue-whiting (Adlandsvik et al. 2001) or sardine and sprat (Coombs et al., 1985), values adjusted by the model agreed with that measured. In contrast for anchovy and sardine in Biscay, measurements performed in 2001 (Boyra et al., 2003) were not in agreement with the vertical distributions sampled in 1996 and 2000 (Motos and Coombs, 2000; Coombs et al., in press). In the case of sardine, sprat and anchovy, individual egg density is constant throughout all egg life span from fertilisation to just before hatching (Coombs et al., 1985; Coombs et al., in press). The egg density is determined in the ovary during the process of oocyte hydration prior to the ovulation. Craik and Harvey (1987) describe how the hydration is triggered by the proteolysis of the yolk proteins generating free amino-acids that increase the osmolarity of the oocyte and consequently generate influx of water in the oocyte from the ovarian fluid. The mechanism could be responsible for adaptating the egg to the ambient sea water density. It is noteworthy that in spring 2001 in Biscay, surface salinity was very low over the entire shelf (31.17 psu) due to very important river discharges in that year in comparison to 1996 (34.64 psu) and 2000 (34.58 psu). Egg density has been reported to vary in relation with sea water density in the Baltic (e.g., Nissling et al., 1996; Solemdal, 1971) as well as seasonally in the Channel (Coombs et al., 1985). It is then hypothesised that the density adaptation mechanism during oocyte hydration could explain the inter-annual density variation found in Biscay for both anchovy and sardine: the egg density would vary with ambient sea water density via the adult fish ovarian osmolarity and consequently the individual egg density would vary according to the particular hydrological spawning condition. To confirm this possibility, the model was used to simulate a greater number of vertical distributions and the egg density was adjusted for the model to best fit the sampled vertical distributions (Table 11). Density values of the different species (sardine, sprat and anchovy) varied in coherence with each other, meaning that there was a similar process across species adapting the egg density. The model-based adjusted egg densities were then plotted against ambient sea water surface density (0-5 m) showing a clear relationship (Fig. 11). As a consequence, it is advised that egg density be considered a variable parameter to be monitored during fisheries surveys together with the hydrological structure. The understanding of the ecological factors determining variation in egg density is a key to model reliably the vertical distribution of fish eggs.

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References

Adlandsvik, B., Coombs, S., Sundby, S. and Temple, G. 2001. Buoyancy and vertical distribution of eggs and larvae of blue whiting (*Micromesistius poutassou*): observations and modelling. Fisheries Research, 50: 59-72.

Boyra, G., Rueda, L., Coombs, S., Sundby, S., Adlandsvisk, B., Santos, M. and Uriarte, A. 2003. Modelling the vertical distribution of eggs of anchovy (engraulis encrasicolus) and sardine (Sardina pilchardus). Fisheries Oceanography, 12(4/5): 381-395.

Checkley, D., Ortner, P., Settle, L. and Cummings, S. 1997. A continuous underway fish egg sampler. Fisheries Oceanography, 6: 58-73.

Checkley, D., Hunter, R., Motos, L. and van Der Lingen, C. 2000. (Eds). Report of a workshop on the use of the continuous underway fish egg sampler CUFES for mapping and spawning habitats of pelagic fish. GLOBEC report 14, 65pp.

Conway, D., Coombs, S. and Smith, C. 1997. Vertical distribution of fish eggs and larvae in the Irish Sea and southern North Sea. ICES Journal of Marine Science, 54: 136-147.

Coombs, S. 1981. A density-gradient column for determining the specific gravity of fish eggs with particular reference to eggs of mackerel *Scomber scombrus*. Marine Biology, 63: 101-106.

Coombs, S., Boyra, G., Rueda, L., Uriarte, A., Santos, M., Conway, D. and Halliday, N. (In press). Buoyancy measurements and vertical distribution of eggs of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*). Marine Biology (published online: 28 may 2004).

Coombs, S., Fosh, C. and Keen, M. 1985. The buoyancy and vertical distribution of eggs of sprat (*Sprattus sprattus*) and pilchard (*Sardina pilchardus*). Journal of the Marine Biological Association of the U.K., 65: 461-474.

Coombs, S., Morgan, D. and Halliday, N. 2001. Seasonal and ontogenetic changes in the vertical distribution of eggs and larvae of mackerel (*Scomber scombrus* L.) and horse mackerel (*Trachurus trachurus* L.). Fisheries Research, 50: 27-40.

Craik, J. and Harvey, S. 1987. The causes of buoyancy in eggs of marine teleosts. Journal of the Marine Biological Association of the UK, 67: 169-182.

Dalavalle, J. 1948. Dynamics of small particles. Pp. 14-40 (Chapter 2) In: Micromeristics: the technology of fine particles. Pitman Publishing Corporation, New York.

Heath, M., Brander, K., Munk, P. and Rankine, P. 1991. Vertical distributions of autumn spawned larval herring (*Clupea harengus* L.) in the North Sea. Continental Shelf Research, 11(12): 1425-1452.

Hutchinson, G. 1967. The hydrodynamics of the plankton. Pp. 245-305 (Chapter 20) In: A treatise of limnology, Vol. II, John Wiley and Sons, New York.

Le Cann, B. 1990. Barotropic tidal dynamics of the Bay of Biscay shelf: observations, numerical modelling and physical interpretation. Continental Shelf Research, 10(8): 723-758.

Lo, N., Hunter, J. and Charter, R. 2001. Use of a continuous egg sampler for ichtyoplankton surveys: application to the estimation of daily egg production of Pacific sardine (*Sardinops sagax*) off California. Fishery Bulletin, 99: 554-571.

Luyten, P., Deleersnijder, E., Ozer, J. and Ruddick, K. 1996. Presentation of a family of turbulence closure models for stratified shallow water flows and preliminary application to the Rhine outflow region. Continental Shelf Research, 16(1): 101-130.

Millero, F. 1974. The physical chemistry of seawater, Ann. Rev. Earth Planet. Sci., 2: 101-150.

Motos, L. and Coombs, S. 2000. Vertical distribution of anchovy eggs and field observations of incubation temperature. Ozeanografika, 3: 253-272.

Nissling, A. and Vallin, L. 1996. The ability of cod eggs to maintain neutral buoyancy and the opportunity for survival in fluctuating conditions in the Baltic Sea. Journal of Fish Biology, 48: 217-227.

Palomera, I. 1991. Vertical distribution of eggs and larvae of *Engraulis encrasicolus* in stratified waters of the western Mediterranean. Marine Biology, 111: 37-44.

Parada, C., van der Lingen, C., Mullon, C. and Penven, P. 2003. Modelling the effect of buoyancy on the transport of anchovy (Engraulis encrasicolus) eggs from spawning to nursery grounds in the southern Benguela: an IBM approach. Fisheries Oceanography, 12: 170-184.

Petitgas, P., Massé, J., Beillois, P., Bourriau, P., Santos, M., Lazure, P. and Planque B. 2002. Estimating in situ daily fecundity by coupling CUFES to acoustics during fisheries surveys: exploration of the methods potential on anchovy and sardine in Biscay. ICES CM 2002/O:3.

Pingree, R., Mardell, G., Holligan, P., Griffiths, D. and Smithers, J. 1982. Celtic Sea and Armorican current structure and the vertical distributions of temperature and chlorophyll. Continental Shelf Research, 1(1): 99-116.

Planque, B., Lazure, P. and Jégou, A.-M. 2003. Interannual variability in spring hydrological changes: a method for typological classification and an application to the Bay of Biscay continental shelf. ICES CM 2003/P:30.

Solemdal, P. 1971. Prespawning flounders transferred to different salinities and the effects on their eggs. Vie et Milieu, 1(Suppl. 22): 409-423.

Stenevik, E., Sundby, S. and Cloete, R. 2001. Influence of buoyancy and vertical distribution of sardine *Sardinops sagax* eggs and larvae on their transport in the northern Benguela ecosystem. South African Journal of Marine Science, 23: 85-97.

Sundby, S. 1983. A one-dimensional model for the vertical distribution of pelagic fish eggs in the mixed layer. Deep Sea Research, 30(6A): 645-661.

Sundby, S. 1991. Factors affecting the vertical distribution of eggs. ICES Marine Science Symposia, 192: 33-38.

Russel, F. 1976. The eggs and planktonic stages of British marine fishes. Academic Press, London, 524pp.

Tanaka, Y. 1992. Japanese anchovy egg accumulation at sea surface or pycnocline: observation and model. Journal of Oceanography, 48: 461-472.

Westgard, T. 1989. Two models for the vertical distribution of pelagic fish eggs in the turbulent upper layer of the ocean. Rapp. P.-V. Réun. Const. Int. Explor. Mer, 191: 195-200.

Williams, R., Collins, N. and Conway, D. 1983. The double LHPR system: a high speed micro- and macroplankton sampler. Deep-Sea Research, 30A: 331-342.

Zeldis, J., Grimes, P. and Ingerson, J. 1995. Ascent rates, vertical distribution and a thermal history model of development of orange roughy, *Hoplostethus atlanticus*, eggs in the water column. Fishery Bulletin, 93: 373-385.

		Salinity (psu)			
		< 30	30 – 32.5	32.5 – 35	> 35
Temperature (°C)	< 10.0	1.477	1.483	1.488	1.495
	10.0 – 12.5	1.369	1.374	1.379	1.385
	12.5 – 15.0	1.282	1.288	1.292	1.298
	15.0 – 17.5	1.196	1.201	1.206	1.211
	17.5 – 20.0	1.125	1.131	1.136	1.145
	20.0 – 22.5	1.055	1.061	1.066	1.070
	22.5 – 25.0	0.998	1.004	1.008	1.013
	> 25.0	0.941	0.946	0.951	0.955

Tableau 1: Dynamic viscosity μ (in centipoise = 10^{-2} g cm^{-1} s^{-1}) of sea water for different ranges of temperature and salinity at normal pressure, after Millero (1974).

	Group 1	Group 2	Group 3	Group 4
CTD Station	F0125	E0372	H0236	F0223
Latitude	47.267	45.665	44.875	45.336
Longitude	-5.205	-1.411	-2.290	-1.666
Date	06 May 2001	24 April 2000	03 June 2003	22 May 2001
Depth (m)	140	25	203	51
Wind (m s^{-1})	9	1.2	6	9
Tide (m s^{-1})	0.55	0.19	0.12	0.17

Table 2: CTD stations closest to hydrodological group centres used for the model sensitivity analysis. Group 1: homogeneous density profile; Group 2: haline stratification; Group 3: thermal stratification; Group 4: haline and thermal stratification.

	Decrease	Reference	Increase
Wind (m s^{-1})	Half of ref	That at CTD station	Double of ref
Tide (m s^{-1})	0.2	0.8	1.3
Anchovy egg diameter (mm)	0.6	0.8	1
Sardine egg diameter (mm)	1.23	1.64	2.05
Anchovy density (sigma-t)	22.63	23.26	23.89
Sardine density (sigma-t)	23.03	23.49	23.94

Table 3: Variation in the input model parameters for the sensitivity analysis. Reference values for wind are that measured at the reference CTD stations (Table 2). Reference values for the egg diameter and density are taken from Coombs et al. (in press) and Boyra et al. (2003). Variations in egg parameters are +/- the standard deviation.

	Decrease	Increase
Impact of wind		
G1	1.99	1.45
G2	5.69	9.67
G3	2.83	2.68
G4	103.28	17.35
Impact of Tide		
G1	0.003	0.009
G2	40.23	1.07
G3	0.002	0.0004
G4	0.0002	0.44
Impact of anchovy diameter		
G1	0.53	0.24
G2	0.92	0.55
G3	0.47	0.20
G4	2.95	2.91
Impact of Sardine diameter		
G1	0.20	0.08
G2	9.86	5.39
G3	0.28	0.13
G4	2.11	1.69
Impact of anchovy density		
G1	0.05	0.08
G2	4.75	488.44
G3	0.06	0.11
G4	15.27	58.384
Impact of sardine density		
G1	0.01	0.02
G2	259.38	603.91
G3	0.03	0.05
G4	19.35	127.19

Table 4: Root mean square difference (RMSD) in the first 50 m the egg profile of the reference run (RR) and that obtained by varying input model parameters for each hydrological group (Tables 2 and 3). G1: homogeneous density profile; G2: haline stratification; G3: thermal stratification; G4: haline and thermal stratification.

	Decrease %	Increase %
Impact of wind		
G1	64.86	-55.79
G2	10	-21.39
G3	49.16	-48.70
G4	-100.00	108.39
Impact of Tide		
G1	1.65	-3.91
G2	187.87	-20.07
G3	1.36	-0.56
G4	0.01	-10.12
Impact of anchovy diameter		
G1	-34.44	23.34
G2	-5.60	3.70
G3	-19.81	13.06
G4	69.17	-46.94
Impact of Sardine diameter		
G1	-13.33	8.56
G2	68.35	-43.74
G3	-10.90	7.88
G4	185.70	-55.96
Impact of anchovy density		
G1	10.35	-13.28
G2	8.62	-100.00
G3	7.13	-9.57
G4	148.30	-89.66
Impact of sardine density		
G1	3.40	-4.04
G2	525.29	-100.00
G3	3.93	-4.73
G4	387.93	-98.44

Table 5: Percent egg in the surface layer (0-5m) in addition or minus relatively to the reference run when the input model parameters are decreased or increased for each hydrological condition (Tables 2 and 3). G1: homogeneous density profile; G2: haline stratification; G3: thermal stratification; G4: haline and thermal stratification.

T-S profile	homogeneous
Depth (m)	600
Wind (m s^{-1})	7.5
Tide (m s^{-1})	0
Sea water surface density (sigma-t)	27.26
Egg diameter (mm)	1.08
Egg density	(sigma-t)
Stage 1	27.34
Stage 2	27.83
Stage 3	28.71
Stage 4	29.20
Egg developmental time	(hours from fertilization)
Stage 1	14.4
Stage 2	38.4
Stage 3	64.4
Stage 4	94.9

Table 6: Model parameters for simulating blue whiting egg distributions (Fig. 6) as reported in Adlandsvik et al. (2001)

	Station 9 (28 may 1996)	Station 10 (28 may 1996)
T-S profile	Important thermal and haline stratification	Slight thermal and haline stratification
Depth (m)	41	38
Latitude	45°33' N	45°22' N
Longitude	1°33' W	1°35' W
Wind (m s^{-1})	1.03	5.14
Tide (m s^{-1})	0.15	0.16
Sea water surface density	23.53	25.35
Egg density (sigma-t) (adjusted)	24.79	24.85
Egg diameter (mm)	0.89	0.89
Characteristic time (days)	1.28	1.23

Table 7: Model parameters for simulating anchovy egg distributions (Fig. 7) as reported in Motos and Coombs (2000). The egg density is adjusted to provide best fit between modelled and observed distributions. The egg diameter is that reported by Boyra et al. (2003). Tide is deduced from station position and date.

	Station 29 (18 may 2000)
T-S profile	Important thermal and haline stratification
Depth (m)	33
Latitude (decimal degrees N)	45°43' N
Longitude (decimal degrees W)	1°43' W
Wind (m s^{-1})	8
Tide (m s^{-1})	0.27
Sea water surface density	23.08
Egg density (adjusted) (sigma-t)	24.55
Egg diameter (mm)	1.64
Characteristic time (days)	0.28

Table 8: Model parameters for simulating sardine egg distribution (Fig. 8) as reported in Coombs et al. (in press). Wind speed and direction are taken from closest Chassiron lighthouse on Île de Ré. The egg density is adjusted to provide best fit between modelled and observed distributions. The egg diameter is that reported by Boyra et al. (2003). Tide is derived from station position and date.

	Station 8 (7 July 1982)	Station 11 (6 October 1982)
T-S profile	Thermal stratification	Homogeneous
Depth (m)	50	50
Latitude	50°15'N	50°15'N
Longitude	4°13'W	4°13'W
Wind (m s^{-1})	8.5	8.4
Tide (m s^{-1})	0.29	0.38
Sea water surface density	25.51	25.71
Egg density (sigma-t)	25.50	25.40
Egg diameter (mm)	1.64	1.64
Characteristic time (days)	1.20	0.67

Table 9: Model parameters for simulating sardine egg distributions (Fig. 9) as reported in Coombs et al. (1985). The wind is taken from the lighthouse of La Hague. The egg density is adjusted to provide best fit between modelled and observed distributions. The egg diameter is that reported by Coombs et al. (in press). Tide is derived from station position and date.

	Station 4 (9 June 1982)
T-S profile	Thermal stratification
Depth (m)	50
Latitude	50°15'N
Longitude	4°13'W
Wind (m s^{-1})	7.4
Tide (m s^{-1})	0.29
Sea water surface density	25.64
Egg density (sigma-t)	26.48
Egg diameter (mm)	0.9
Characteristic time (days)	3.34

Table 10: Model parameters for simulating sprat egg distribution (Fig. 10) as reported by Coombs et al. (1985). The wind is taken from the lighthouse of La Hague. The egg density is adjusted to provide best fit between modelled and observed distributions. The egg diameter is that reported by Russel (1976). Tide is derived from station position and date.

Station Date	Reference	Surface water density (sigma-t)	Anchovy egg density (sigma-t)	Sardine egg density (sigma-t)	Sprat egg density (sigma-t)s
St 04 9 June 1982	Coombs et al. (1985)	25.7255	-	-	26.48
St 05 16 June 1982	Coombs et al. (1985)	25.5316	-	25.86	26.05
St 08 07 July 1982	Coombs et al. (1985)	25.5336	-	25.505	26
St 11 06 October 1982	Coombs et al. (1985)	25.7147	-	25.4	-
St 06 27 May 1996	Motos et al. (2000)	25.304	25.35	-	-
St 09 28 May 1996	Motos et al. (2000)	24.3351	24.795	-	-
St 10 28 May 1996	Motos et al. (2000)	25.2349	24.85	-	-
St 12 29 May 1996	Motos et al. (2000)	26.3658	26.45	-	-
St 15 09 May 2000	Coombs et al. (in press)	26.1703	26.167	26.15	-
St 29 18 May 2000	Coombs et al. (in press)	23.1224	24.5	24.55	-

Table 11: Model-based adjusted egg densities and sea surface (0-5 m) water density at different stations taken from the literature.

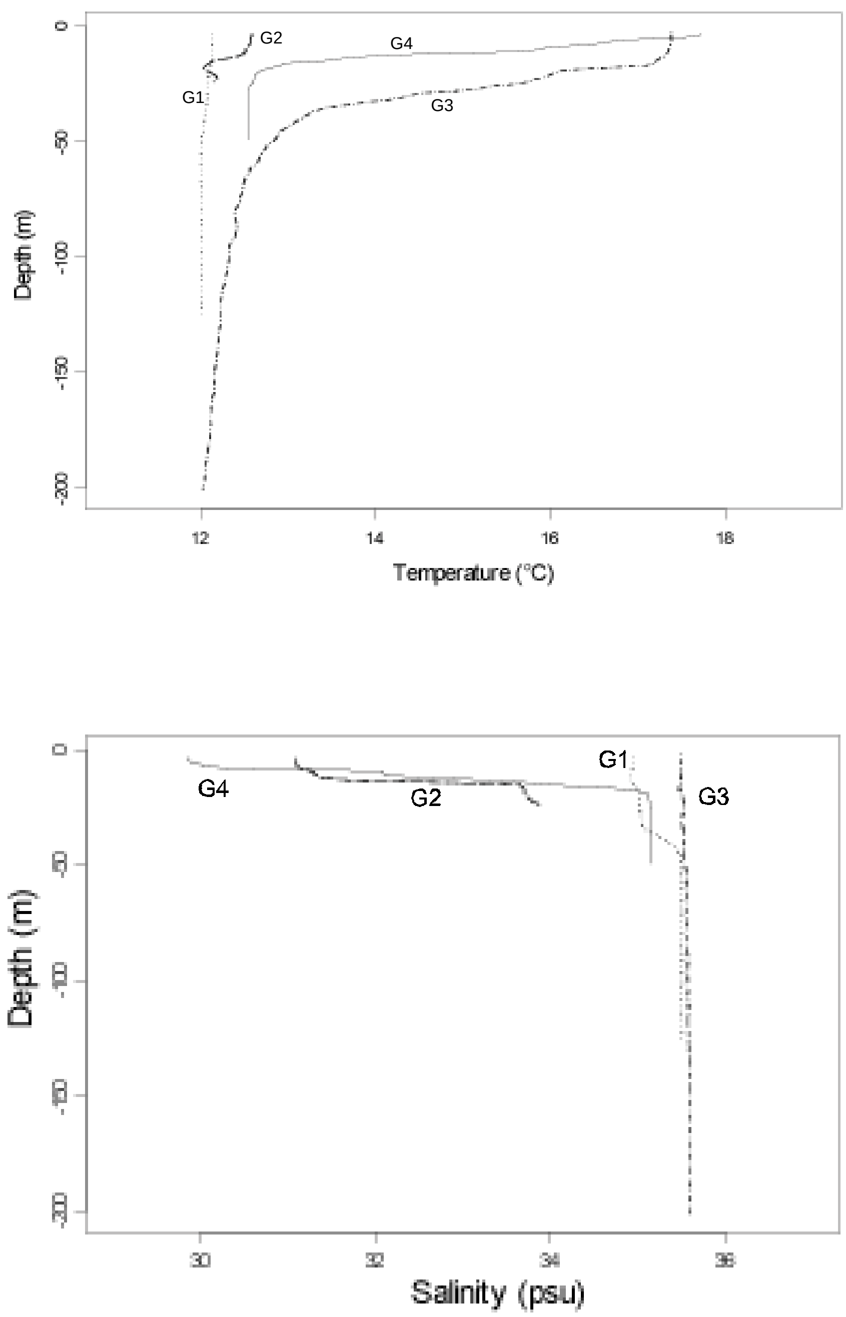


Figure 1: Profiles of temperature (top) and salinity (bottom) typical of hydrological spring situations in Biscay French shelf (hydrological groups). G1: homogeneous density profile; G2: haline stratification; G3: thermal stratification; G4: haline and thermal stratification.

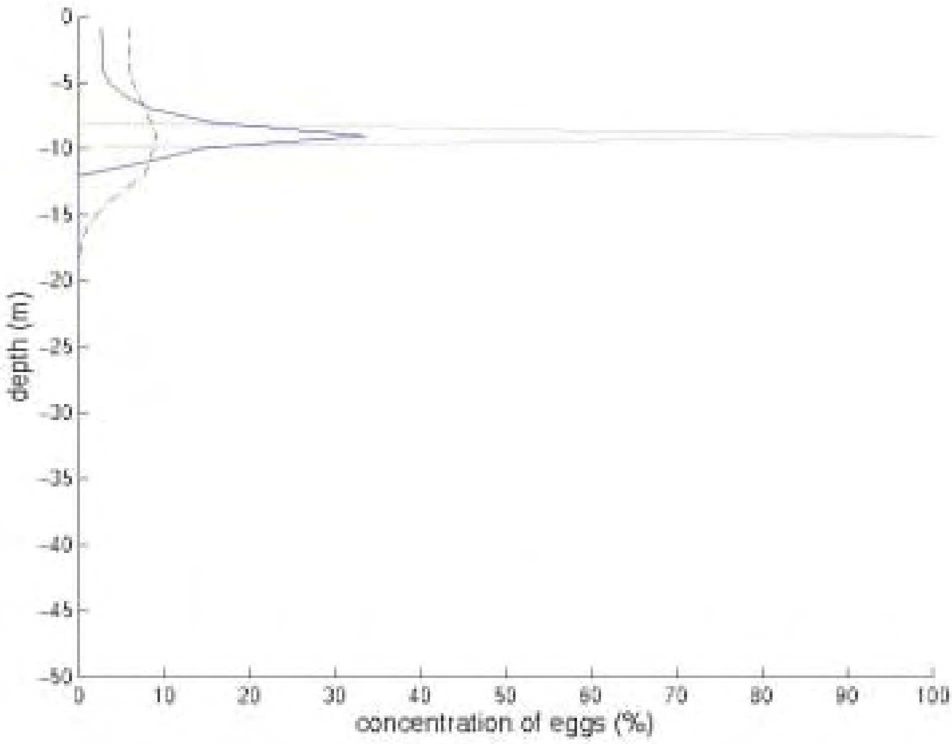


Figure 2: Sensitivity of anchovy steady-state distribution to variations in wind condition for hydrological group G4 (haline and thermal stratification). Continuous line : Reference Run; dotted line: decrease; dashed line: increase. Model parameter values are in Tables 2 and 3.

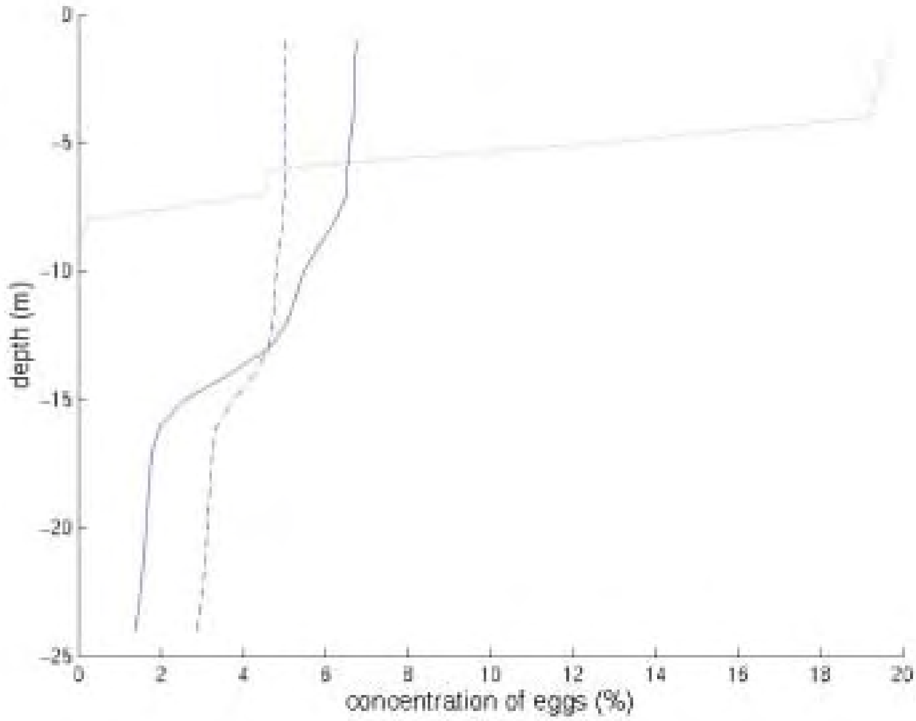


Figure 3: Sensitivity of anchovy steady-state distribution to variations in tide condition for hydrological group G2 (haline stratification). Continuous line : Reference Run; dotted line: decrease; dashed line: increase. Model parameter values are in Tables 2 and 3.

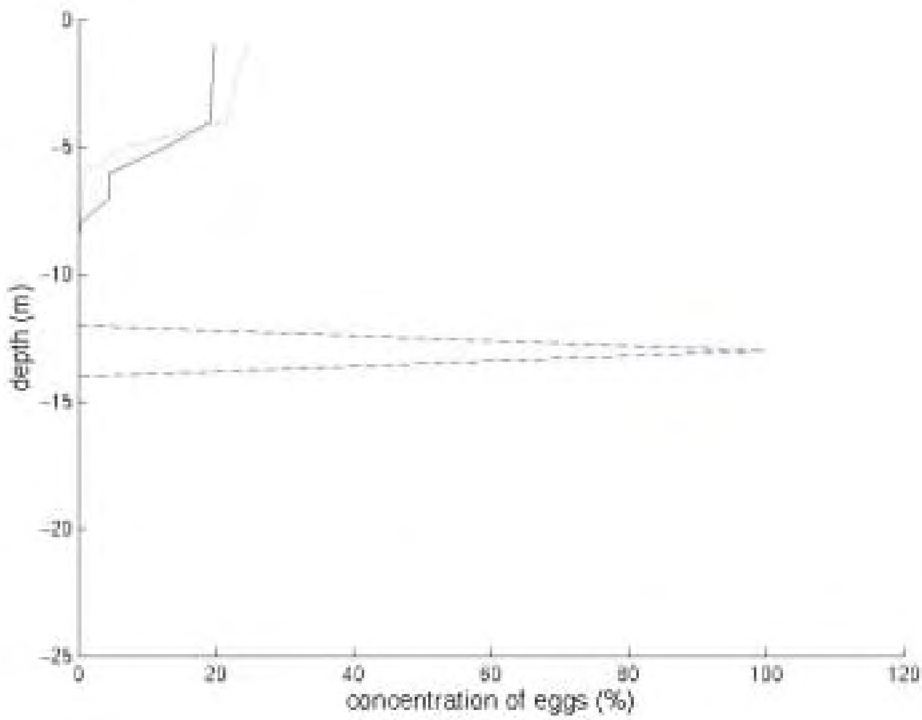


Figure 4: Sensitivity of anchovy steady-state distribution to variations in anchovy egg density for hydrological group G2 (haline stratification). Continuous line : Reference Run; dotted line: decrease; dashed line: increase. Model parameter values are in Tables 2 and 3.

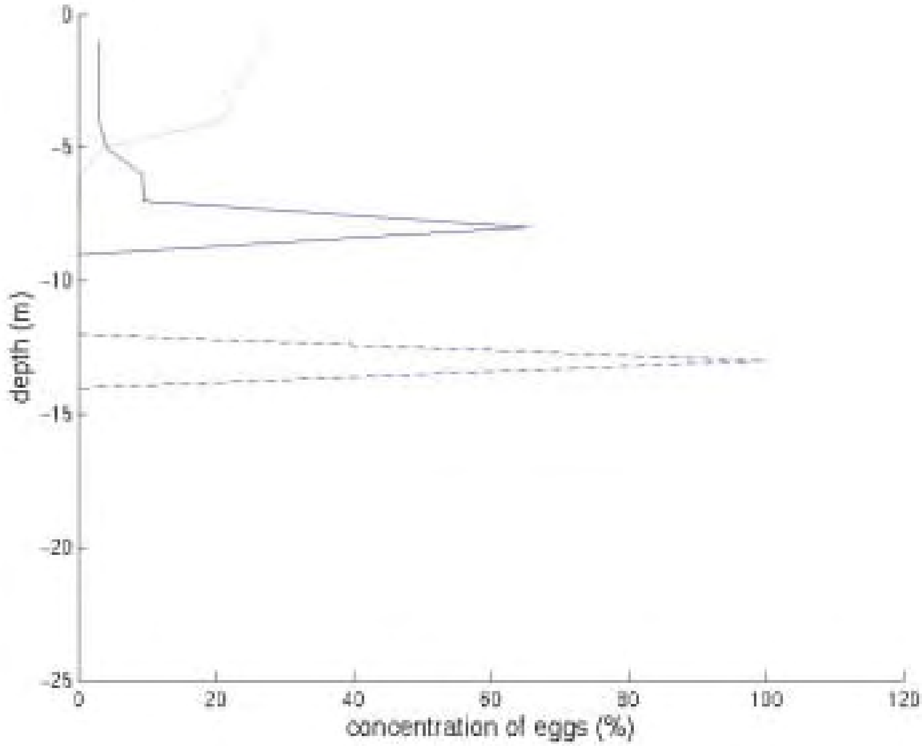


Figure 5: Sensitivity of sardine steady-state distribution to variations in sardine egg density for hydrological group G2 (haline stratification). Continuous line : Reference Run; dotted line: decrease; dashed line: increase. Model parameter values are in Tables 2 and 3.

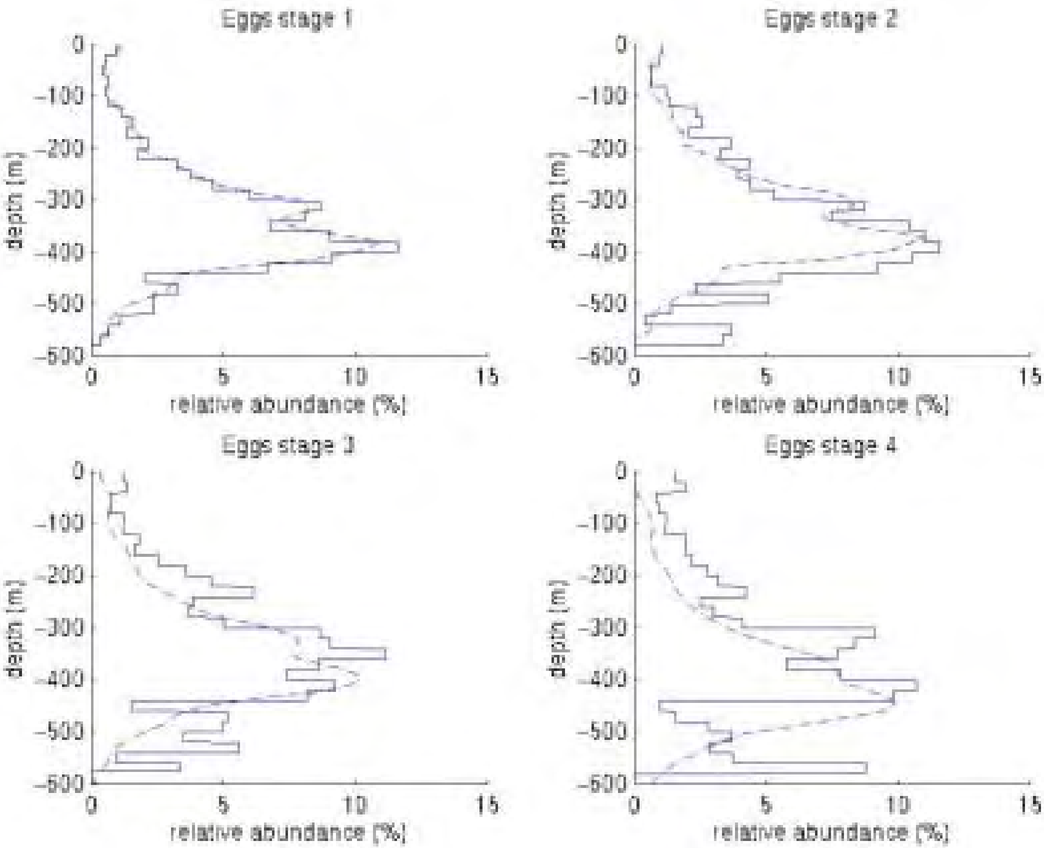
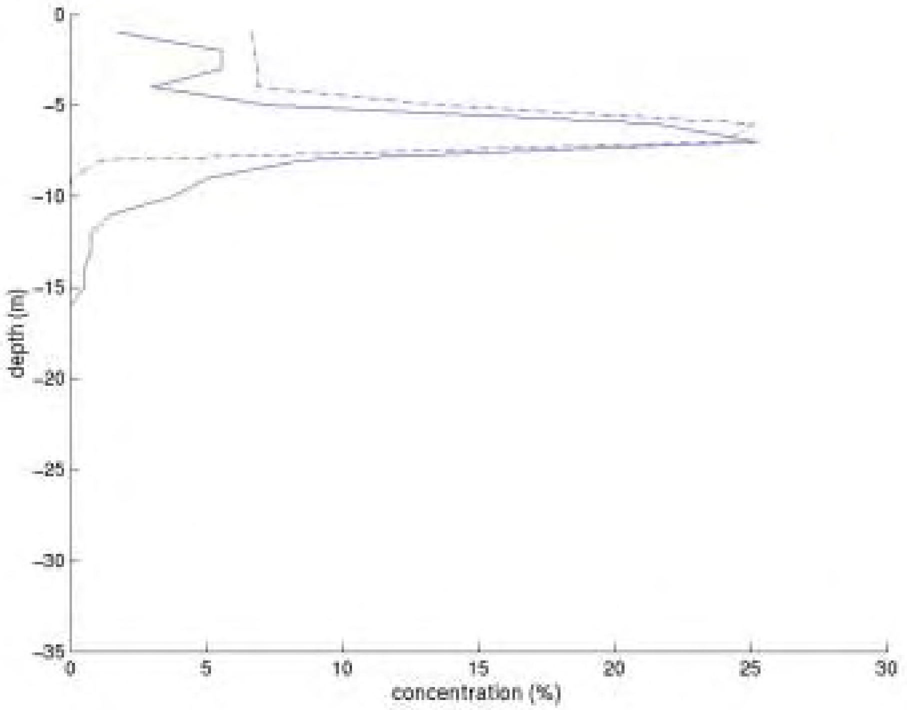


Figure 6: Vertical distribution of blue whiting eggs at different developmental stages (Adlandsvik et al, 20001). Continuous line: sampled distribution; dotted line: modelled distribution. Model parameter values are in Table 6.



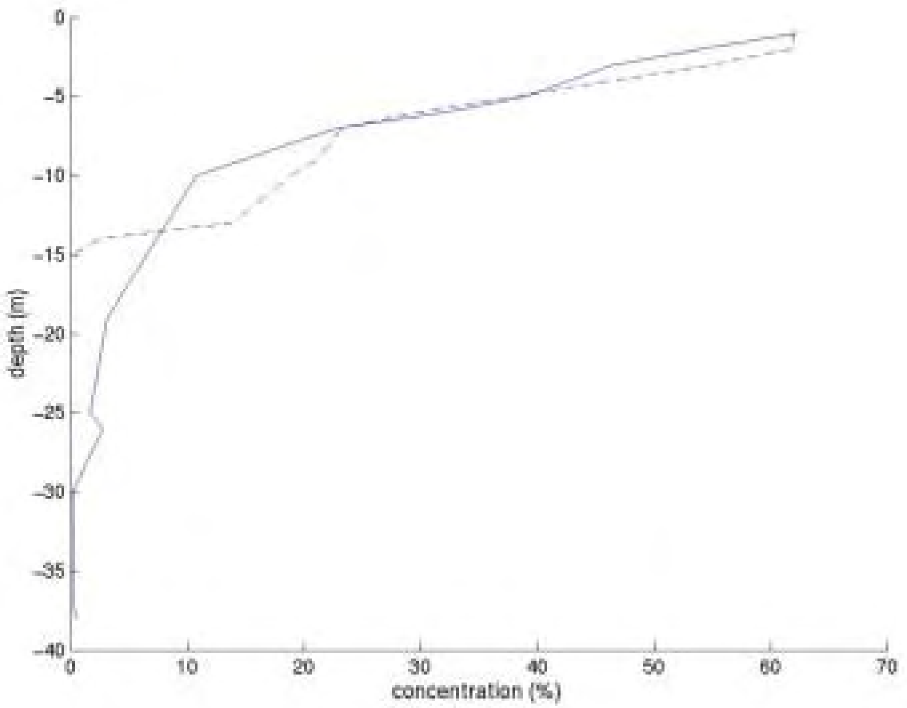


Figure 7: Vertical distributions of anchovy eggs (Motos and Coombs, 2000) at station 9 (28 mai 1996) (top) and station 10 (28 mai 1996) (bottom). Continuous line: observed distribution. Dotted line: modelled distribution. Model parameters are in Table 7.

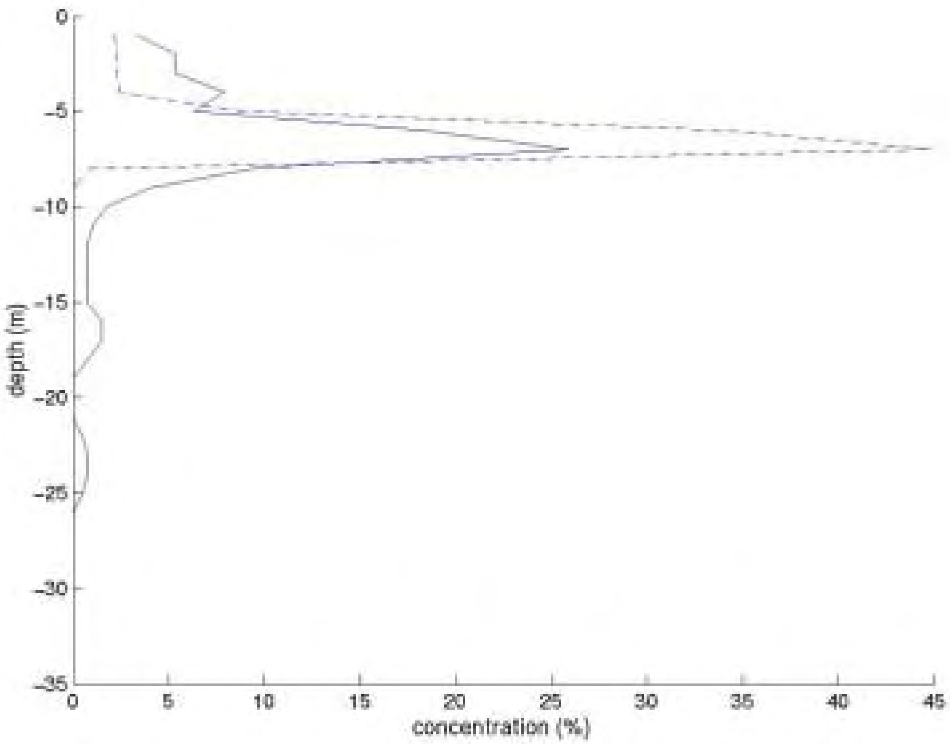


Figure 8: Vertical distribution of sardine eggs (Coombs et al., in press) at station 29 (18 mai 2000). Continuous line: observed distribution. Dotted line: modelled distribution. Model parameters are in Table 8.

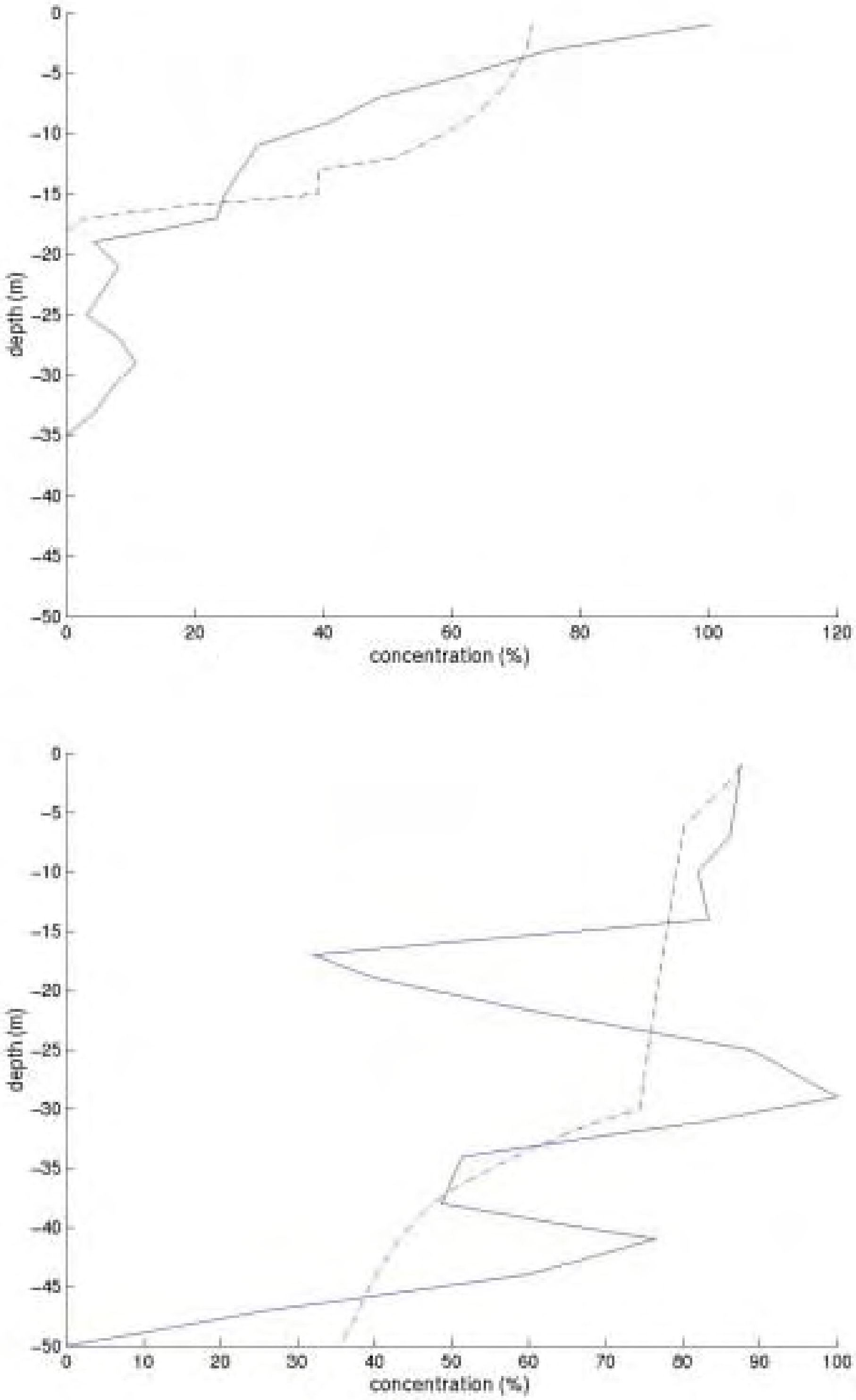


Figure 9: Vertical distributions of sardine eggs (Coombs et al., 1985) at station 8 (07 juillet 1982) (top) and station 11 (06 Octobre 1982) (bottom) Continuous line: observed distribution. Dotted line: modelled distribution. Model parameters are in Table 9.

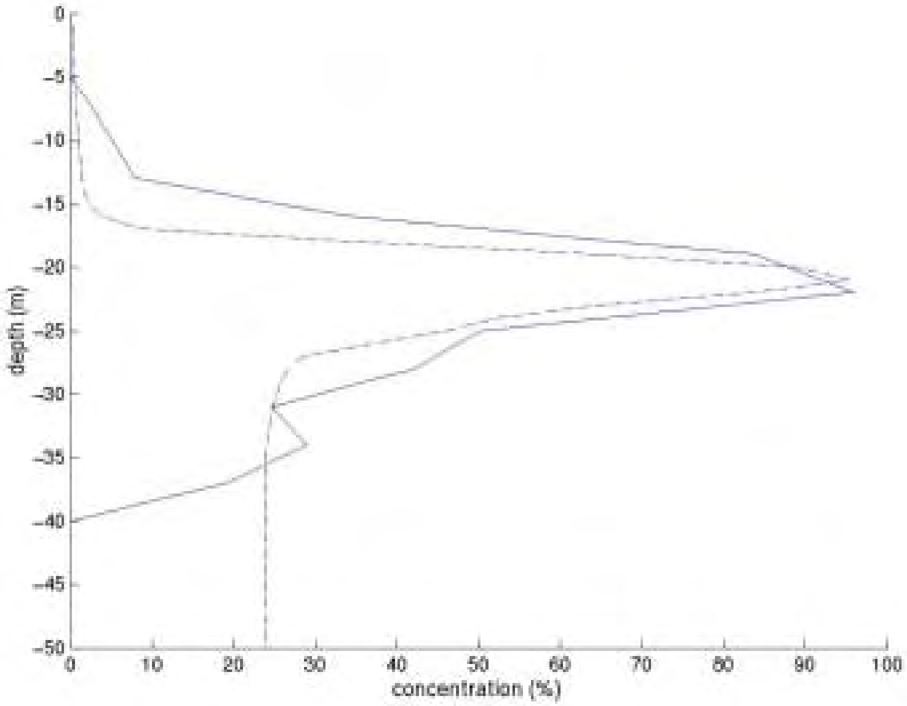


Figure 10: Vertical distribution of sprat eggs (Coombs et al., 1985) at station 4 (09 juin 1982). Continuous line: observed distribution. Dotted line: modelled distribution. Model parameters are in Table 10.

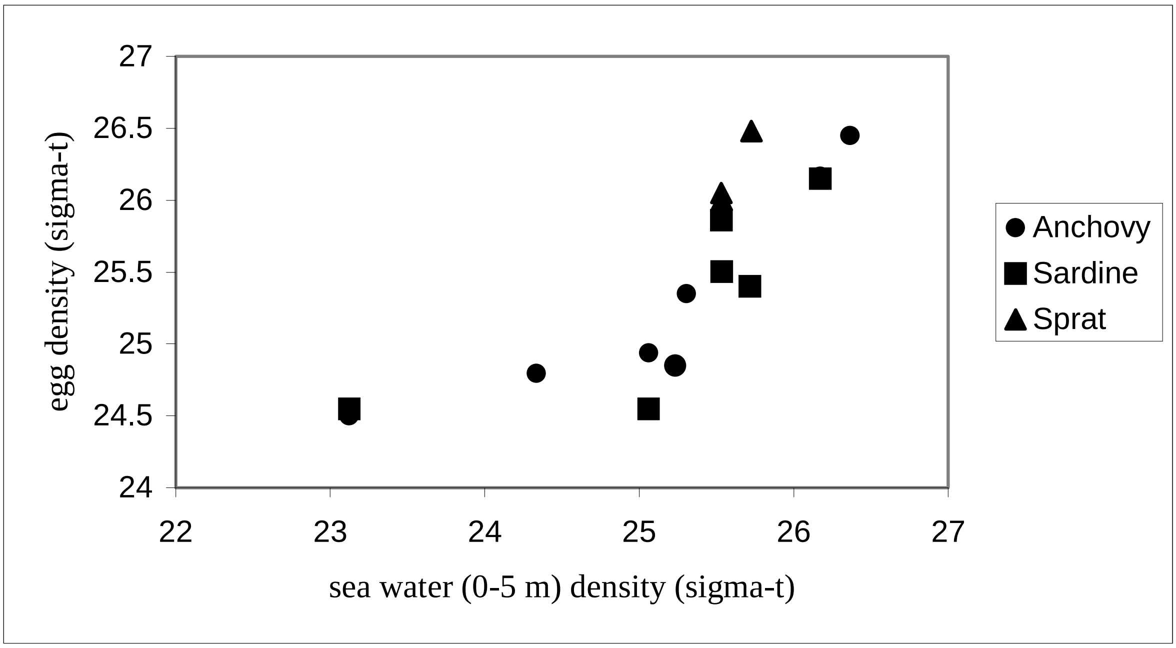


Figure 11: Relationship between the density of ambient sea surface (0-5m) water density and that of the egg density. The egg density was adjusted for the model to best fit the sampled vertical distributions (Tables 11).