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Impact of a winter upwelling event on the distribution and transport of sardine (*Sardina pilchardus*) eggs and larvae off western Iberia: a retention mechanism

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Abstract

A hydrographic and ichthyoplanktonic survey was conducted on the western Iberia Peninsula shelf-slope, with the objective of assessing the influence of wind-driven flow on the transport and survival of sardine early life history stages. Measurements were taken during a 2-week period of an ‘upwelling-favourable’ wind event. An offshore displacement of the surface low salinity Western Iberia Buoyant Plume (WIBP) was observed well off the shelf break. Below the plume, the current was southward over the mid- and inner-shelf. Offshore, the flow was poleward in the northern part of the survey area and equatorward in the south. A convergence zone was detected along the outer shelf and upper slope where the buoyant plume was apparently trapped and deepened. In general, eggs and larvae were distributed according to the spreading of the low salinity surface waters, and also within the convergent band. Older larvae were retained within the latter feature. The role of wind forcing on the plume and its interaction with the slope flow were analysed. A mechanism of larvae retention was formulated based on simplified models of the observed shelf-slope circulation.

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1. Introduction

Over the last decades significant changes in the upwelling patterns off the Portuguese west coast have been observed (e.g., Santos et al., 2001; Borges et al., 2003), namely an increase in upwelling events in winter due to an increase in the frequency and intensity of equatorward winds

observed since the end of the 1960s (Borges et al., 2003).

The maximum intensity of sardine (*Sardina pilchardus* Walbaum, 1792) spawning off Portugal takes place predominantly from November through April (Figueiredo and Santos, 1989; Ré et al., 1990; Zwolinski et al., 2001). The reproductive strategies of some pelagic fish adapted to coastal upwelling ecosystems, such as sardine on the Portuguese west coast, have developed to minimise Ekman offshore transport effects and assure shoreward transport and larval retention

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(e.g., Roy et al., 1989). Therefore, an increase in upwelling events during the spawning period may have a negative impact on sardine recruitment because of the increased larval mortality through offshore transport into unfavourable areas.

Santos et al. (2001) found statistically that the intensity and frequency of upwelling events during the spawning season (winter) does indeed have a negative impact on the recruitment of small pelagic species off the west coast of Portugal, limiting its success even if beneficial upwelling conditions occur later during the summer upwelling (feeding) season. Stratoudakis et al. (2003) also found a significant reduction in the sardine spawning area in north-western Portugal in the late 1990s.

To test the hypothesis that the occurrence of upwelling events during the spawning season (winter) can significantly affect the distribution of sardine early life stages and their survival, an observational programme was conducted off northern Portugal in February 2000.

The distribution and offshore transport of sardine eggs and larvae may not be determined only by wind action. Other local features constrain the surface response to coastal upwelling; namely the Western Iberia Buoyant Plume (WIBP) (Peliz et al., 2002), the Iberian Poleward Current (IPC) (Peliz et al., 2003b) and its associated mesoscale structures, as well as the interaction between the poleward flow and the buoyant plume.

The aim of this paper is to present the results of the observed distribution and abundance of sardine eggs and larvae in relation to the main ocean features of the upper layer and shelf waters during an upwelling event. To simulate the major patterns of eggs and larval transport a derived two-dimensional flow field was calculated, based on simplified estimates of the circulation features during the survey, and a set of Lagrangian particles are tracked in the sampled area. Finally, a conceptual model of the retention mechanism is presented and discussed.

2. Study area, data and methods

The SURVIVAL'2000 cruise (02040200) took place off the northwest Portuguese coast onboard

IPIMAR's R/V *NORUEGA*. Five transects were made perpendicular to the coast between Viana do Castelo (41.6°N) and Figueira da Foz (40.4°N) from February 16 to 20, 2000 (Fig. 1). Two current meter mooring arrays were deployed at the beginning of the survey.

Hydrographic parameters were measured at all the stations using a SBE 9p CTD in its first use after factory calibration with a sampling rate adjusted to 12 or 24 scans every second and a lowering rate of about 1 m/s. Chlorophyll concentrations were measured with a Seapoint fluorometer coupled to the CTD. Water samples for calibration were collected in all stations with a carousel sampler. Water salinity was measured in the laboratory using a Guideline Autosol 8400B Salinometer. A total of 365 salinity samples were

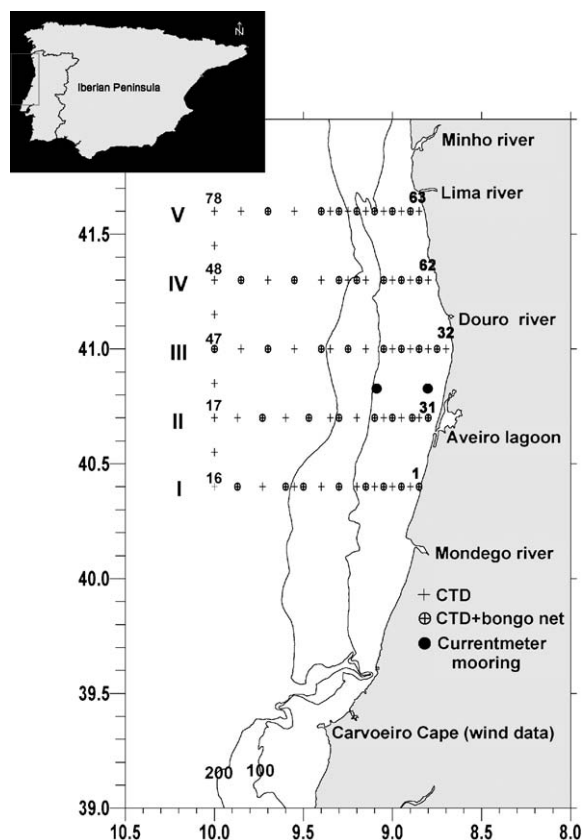


Fig. 1. Study area (northwestern Portuguese coast), cruise sampling grid and current meter mooring location. The 100 and 200 m bathymetry lines are shown.

used to calibrate the conductivity data. Standard algorithms (Fofonoff and Millard, 1983) were used to compute salinity and density. Fluorometer data were calibrated according to the methodology described in Ribeiro et al. (submitted for publication).

Current meter data were obtained with three Aanderaa RCM 9 instruments in two mooring arrays: one deployed over the 80 m isobath with two current meters at depths of about 20 and 50 m, respectively; and the second over the 30 m isobath with one current meter at about 20 m depth. The data were low-pass filtered to remove tidal and inertial oscillations and the final time series represent the residual currents.

Fish eggs and larvae were sampled using a bongo net of 60 cm mouth diameter fitted with 500 and 335 μm mesh nets. A single Hydro-Bios flowmeter was fitted on the side of the 335 μm mesh net to compute the volume of water filtered during each haul. All hauls were taken at a speed of 2 knots. Sampling was carried out to a maximum depth of 50 m, or about 5 m above the bottom where the water depth was shallower. A total of 97 oblique hauls were obtained at selected stations (Fig. 1). Plankton samples (335 μm) were fixed immediately after collection with 4% buffered formalin. In the laboratory, fish eggs and larvae were sorted and counted. Larval lengths were measured with the aid of a binocular microscope to the nearest 0.5 mm by placing the larva on a transparent grid marked in millimeters

and illuminated from below. All larval lengths correspond to standard lengths corrected for shrinkage (live length) according to Theilacker (1980).

3. The wind event and circulation at the slope

The wind during 15 January to 15 March 2000 at the meteorological station of Cape Carvoeiro (Portuguese Meteorological Office) is presented in Fig. 2. This station is located several tens of kilometres to the south of the sampled area but no important differences over this distance are expected in the wind fields. The most significant southward upwelling event started a few days before the cruise and had a duration of about 2 weeks, including a slight relaxation around 20 February. Although persistent in direction, the wind intensity was not very strong, with maximum velocities of about 5–8 m/s. Before the cruise the wind varied mainly between episodes of southerly and southeasterly winds, but with lighter intensity.

Fig. 3 is an attempt to collect together the most important features capable of influencing the surface circulation and the transport patterns. The horizontal distribution of temperature at 100 m, the shallowest level out of the influence of the surface buoyant plume (Fig. 3a), and the corresponding geostrophic velocity field at 100 m calculated relative to the 1350 dbar level (under the Mediterranean water main core) show the three

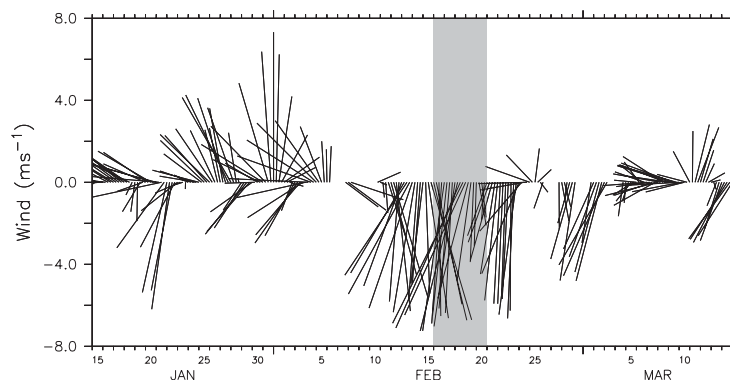


Fig. 2. Stick diagram of wind (m/s) measured at Cabo Carvoeiro (9.40°W; 39.36°N) by the Portuguese Meteorological Office between 15 January and 15 March 2002 (negative values correspond to north winds).

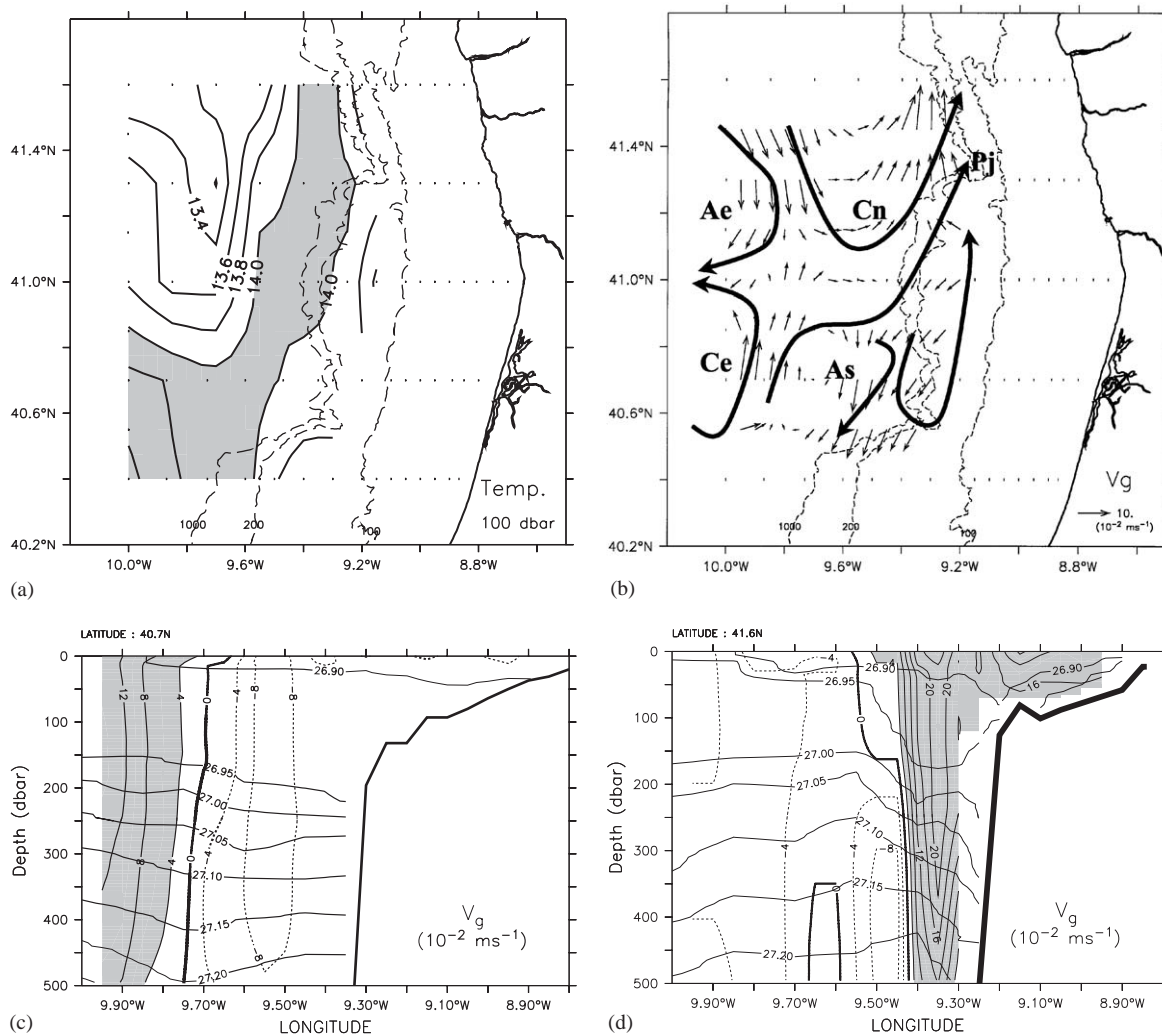


Fig. 3. Horizontal distributions of (a) temperature at 100 dbar (°C; values > 14°C are in shaded) and (b) geostrophic velocity (cm/s) referred to 1350 dbar at 100 m depth, and vertical fields of geostrophic velocity (cm/s) referred to 1350 dbar superimposed in density fields (σ_t) for (c) section II (40.7°N) and (d) section V (41.6°N). Poleward flow is shaded in vertical fields. Cn and Ce represent cyclonic eddies, Ae and As represent anticyclonic eddies, and Pj is the poleward slope jet (see text for details).

most prominent circulation features (Fig. 3b). The first is an anticyclone in the south (As—centred at about 9.8°W and 40.7°N) coincident with a zone of warm waters. This feature induces southward flow over the slope in the southern half of the sampled area as seen in the geostrophic velocities in section II (Fig. 3c). At the same time, a cyclonic meander (Cn—centred at about 9.6°W, 41.4°N) associated with a cold intrusion (Fig. 3a,b) and a poleward slope jet (Pj) with velocities up to

0.25 m/s, transporting warmer and saltier waters northward, dominated the northern part of the survey (Fig. 3d). An additional cyclone–anticyclone pair seaward of the first structures was also detected. Here, the cyclone was in the south (Ce) and the anticyclone in the north (Ae).

These circulation structures are not strongly influenced by the wind event, but have a significant influence on the response of the surface layer as discussed below. The most relevant contribution is

the meridional advection of the plume waters that are transported off the shelf by the Ekman dynamics. In the northern part, the poleward slope jet is strong enough to constrain Ekman transport, as will be seen later, in contrast to the southern area, where the flow is broader and slower.

4. Response of the upper layer and buoyant plume dynamics

The WIBP is a low salinity surface water fed by the winter-intensified runoff of several rivers on the northwest coast of Portugal and Spain (Fig. 1, Minho, Mondego, Douro, Lima, Vouga). During typical non-upwelling winter conditions, the plume is confined to the inner-shelf from the Mondego river mouth northward with salinity values less than 35.7–35.8 psu (Peliz et al., 2002). Salinity minima are variable and are usually located in patches close to the estuaries. Because of their higher buoyancy, the surface waters in the plume also exchange heat with the atmosphere in a different way from the surrounding waters as the thermally driven convection is limited to a thinner layer. This contributes to a faster cooling of plume waters, which are usually cooler at their estuarine source. This leads to the plume waters having lower temperatures than surrounding offshore waters and they may even be colder than the waters beneath. This thermal contrast between plume and oceanic waters is enhanced when the IPC is intensified, as this current transports warmer and saltier waters poleward along the slope.

The most remarkable observation in the surface hydrographic fields is the unusual offshore extension of the WIBP (Fig. 4), as a first consequence of the seaward transport of low salinity surface waters (minimum <35.2) inside the surface Ekman layer. However, the plume is not transported offshore as a continuous feature, as its separation from the coast is detected only in a narrow band less than 20 km wide as verified by the presence of salinity values above 35.7 near the shore (e.g., Fig. 4b). Its offshore extension is about 100 km, in the centre of the sampling area, and it is separated into

two main patches located just offshore of the shelf break, one at 9.4°W, 40.7°N and the other at 9.2°W, 41.6°N. This means that factors other than offshore advection are involved in the response of the plume to the upwelling-favourable winds.

The observed patches may have originated at the coast as pools of direct river output in the vicinity of the river mouths; however, their evolution most likely resulted from the interaction of the stratified Ekman layer with the circulation at the slope. The Ekman dynamics cause an offshore displacement of the plume crossing the upper slope current ageostrophically and, in turn, the poleward flow forces a northward advection. Moreover, the several mesoscale features associated with the poleward current will condition the further advection and mixing of the plume.

The zone where the plume is disrupted (9.6°W, 41.2°N; Fig. 4b) coincides with the cyclonic meander, whereas the larger patch of the plume in the south coincides with the anticyclone observed over the slope (Fig. 3b). The plume is generally evident northward and coastward along the flow of the IPC.

Once beyond the slope, the plume interacts with the offshore cyclone and anticyclone. These create a confluence zone between them that is coincident with the westernmost limit of the plume (at about 9.8°W, 41.0°N). Ribeiro et al. (submitted for publication) in a sequential analysis of satellite-derived pigment concentrations, detected the offshore advection of the high-pigment-concentration plume, which is schematically represented in Fig. 5. The plume expands offshore and its maximum offshore extension is coincident with a filament located in the confluence zone described above with maximum velocities of 29.3 km/day (Ribeiro et al., submitted for publication). Elsewhere, the seaward advection of the front was obstructed by the along-slope flow.

In general, the plume is thicker on its coastward side (note the salinity and density distributions in the various sections of Figs. 6 and 7). This type of structure is generated in the process of plume advection forced by Ekman layer dynamics. Fong and Geyer (2001) modelled the response of a buoyant plume to upwelling-favourable wind and found an asymmetry between the front and the

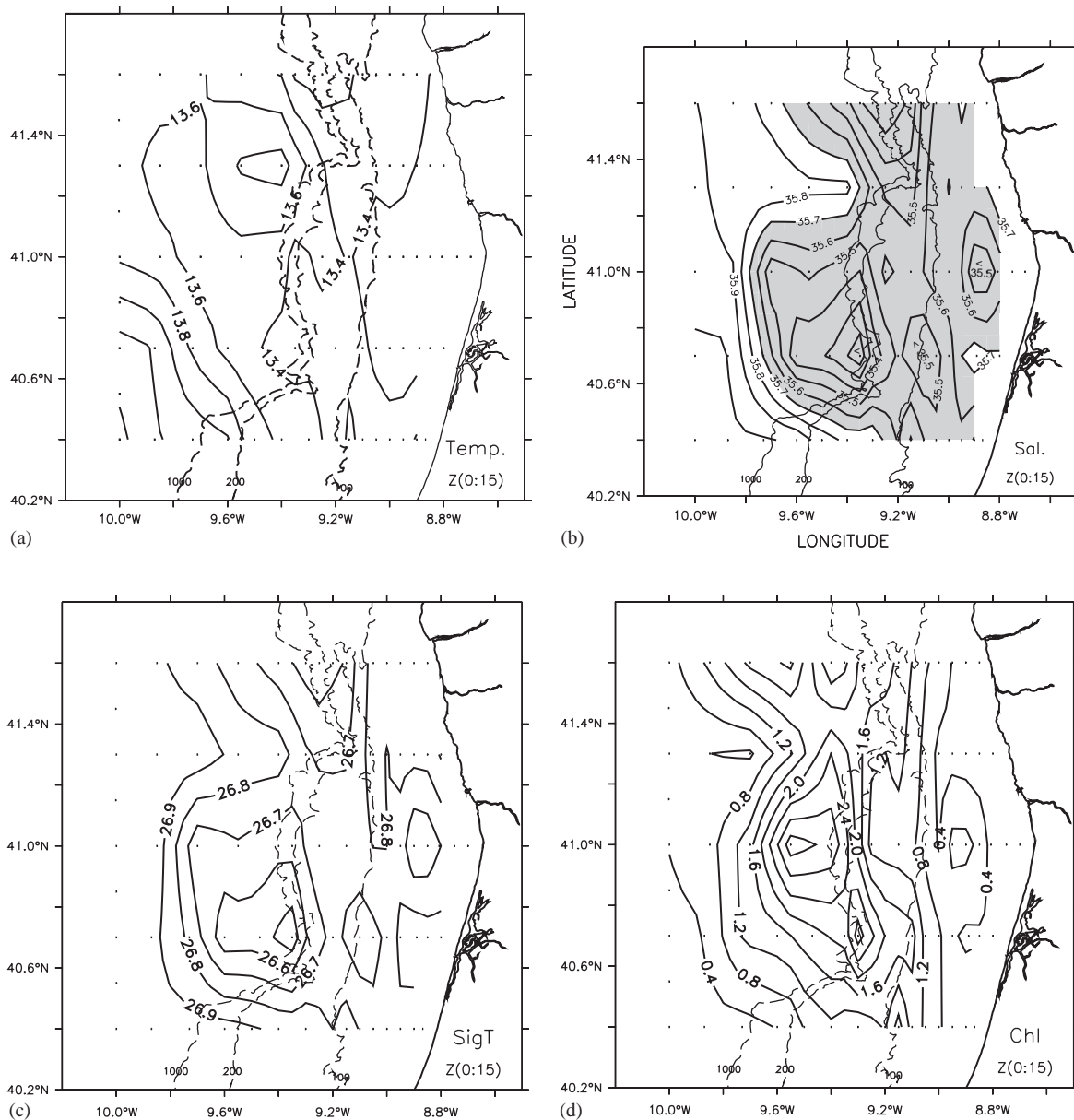


Fig. 4. Horizontal distributions (0–15 m) of (a) temperature ($^{\circ}\text{C}$), (b) salinity, (c) density (σ_t), and (d) chlorophyll-*a* concentration (mg/m^3). The WIBP is shaded in (b).

rear side of the plume. The seaward side tends to become more stratified once lighter plume waters are advected above the denser offshore waters. This increase in the stratification makes the Ekman layer thinner (e.g., Lentz, 1992; Price and Sundermayer, 1999). The inner side of the plume

has a different evolution. Ekman transport brings denser waters into the plume, which then overturns, deepens and gains volume by mixing with deeper waters. This process is repeated until the coastward side of the plume becomes significantly mixed as in the example of section IV (Fig. 7b).

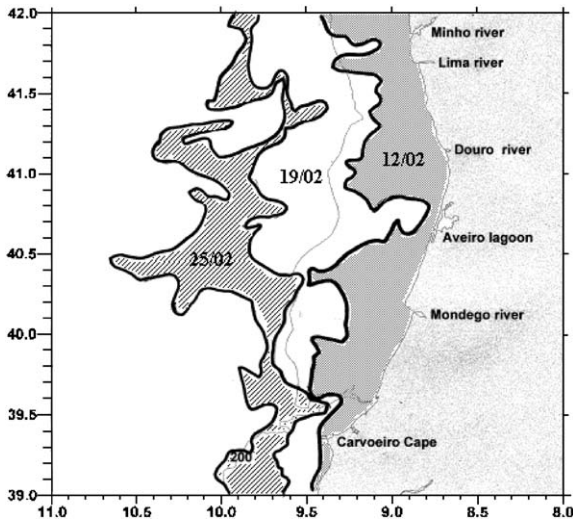


Fig. 5. Spatial and temporal progression of the chlorophyll-*a* front derived from ocean colour satellite data (SeaWiFS sensor onboard Orb View-2 satellite), on 12, 19 and 25 February 2000. The thin line represents the 200 m isobath (adapted from Ribeiro et al., submitted for publication).

Another important component of the upper layer response to the upwelling event concerns the phytopigment concentration growth (Fig. 6d). The Ekman layer was nearly coincident with the stratified upper layer and almost all the surface transport consisted of a westward advection and horizontal spreading of the plume, with little entrainment of the offshore deep mixed layer. This provided a vertical retention mechanism that constrained the biological response of the system in an unexpected way, in view of the typical winter response of deep (100–150 m) low-nutrient mixed layers. Thus, the offshore concentration of phytoplankton is relatively high. Ribeiro et al. (submitted for publication) registered a significant growth proportional to the enlargement of the plume area. This phytoplankton development was supported by the stratification maintained in the process of offshore advection of the plume, as becomes obvious in the comparison between the surface phytopigment concentrations (Fig. 4d) and the stratification inside the plume (Fig. 8). A more detailed discussion about the process of phytoplankton biomass response to the upwelling event

can be found in Ribeiro et al. (submitted for publication).

5. The inner shelf and the convergence zone

Over the inner shelf, southward flow directly measured by the three current meters placed on the two moorings show that the upwelling event had two main bursts with a short relaxation in between (Fig. 9). The intensities indicate that the event was significant, although no strong upwelling jets were generated (maximum sub-inertial values are about 0.15 m/s southward in the inner mooring—not shown). However, despite the evidence of upwelling, the surface plume waters were not completely advected off the shelf. Indeed, as some were transported offshore, others were advected southward along the shelf. This picture contrasts with the one described before, for the outer shelf, where a northward flow was observed in the northern part of the slope. This change of flow direction observed at the outer shelf is associated with a convergence band oriented along-coast that extends throughout all the sampled area.

In the vertical distributions (Figs. 6 and 7), the interaction between the plume and the IPC is evident. As the plume expands offshore, it will interact with the poleward flow creating conditions for a convergence at the surface. The mechanism for convergence results from the fact that the along slope flow acts as a barrier to the surface Ekman transport. The poleward flow is intense and perpendicular to the Ekman transport and it is expected that part of the plume be retained there. However, if the wind-driven surface transport is significantly intense and persistent, the shelf waters can cross over the poleward current. Fig. 6a is a good example of this interaction: the plume waters are cooler than the poleward flow, which can be identified by the closed 14°C temperature contour.

Another factor likely to contribute to the retention of the plume is the vertical circulation associated with the upwelling dynamics. In the case of a deep mixed layer and moderate along-shore currents, replacement of the surface waters is done from the interior layer (e.g., Allen et al.,

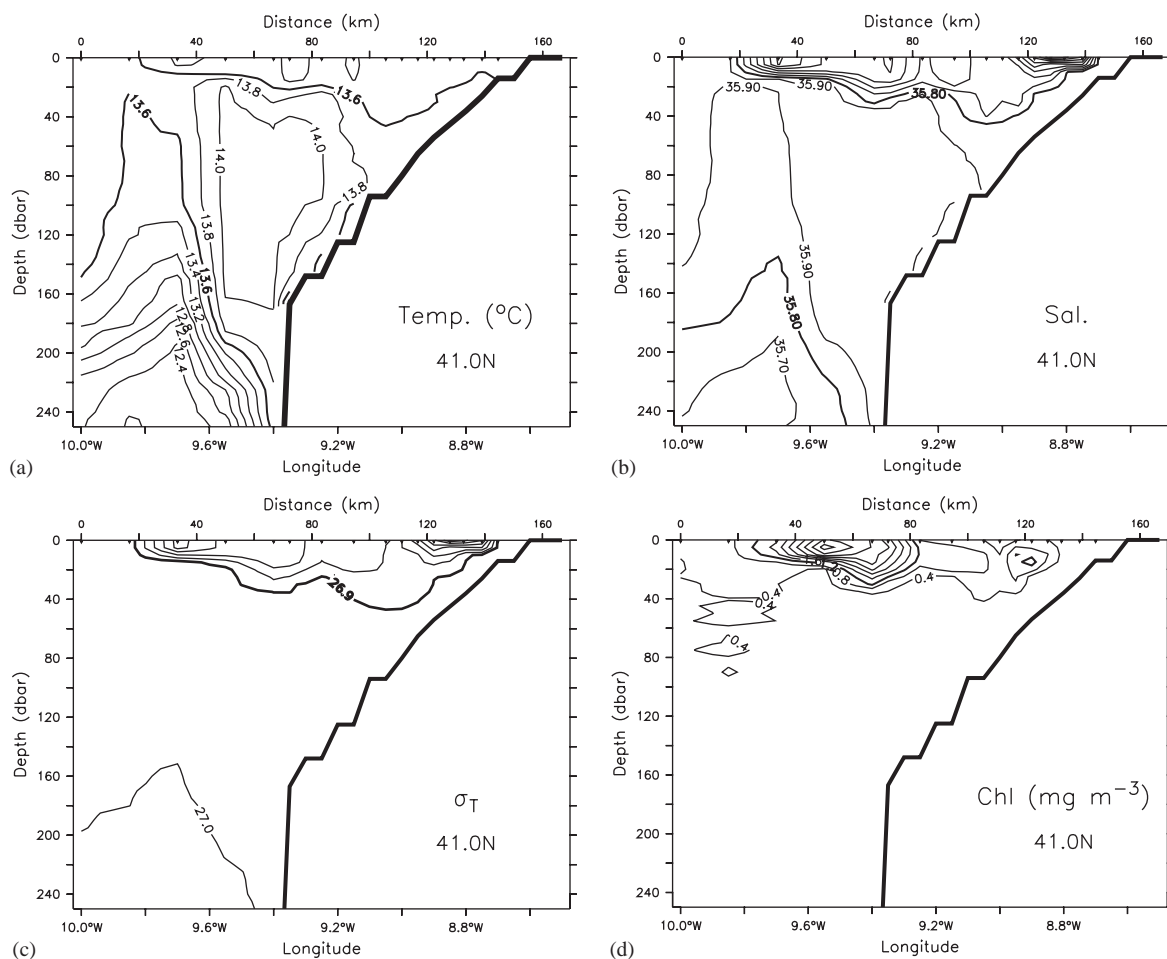


Fig. 6. Vertical fields of section III (41.0°N): (a) temperature (°C), (b) salinity, (c) density (σ_t), and (d) chlorophyll-*a* concentration (mg/m^3).

1995), and the vertical circulation is closed at the outer shelf through a surface convergence of the upwelled waters. A deepening of the plume close to the outer shelf was observed throughout the sampled area and is coincident with the change in the slope of the isopycnals. This pattern can be seen in the topography of the 35.8 isohaline surface (considered to be an indication of the deepest limit of the plume) in Fig. 10. In the northern half of the sampled area this shelf zone also coincides with a change in the direction of the along-shore flow: northward at the upper slope and southward from the mid-shelf up to the coast.

The plume deepens in the outer shelf more remarkably in the northern part where the poleward slope flow is increased (see the maximum of 55 m at about 9.1°W, 41.3°N in Fig. 10). This indicates that bottom Ekman layer dynamics, as described in Peliz et al. (2003a), may contribute to the generation of this convergence band. These authors conducted a numerical study of the response of the shelf/slope system with an along-slope current to upwelling-favourable winds, similar to the situation described here. They found that a divergence in the bottom Ekman layer occurs due to the change in orientation of the

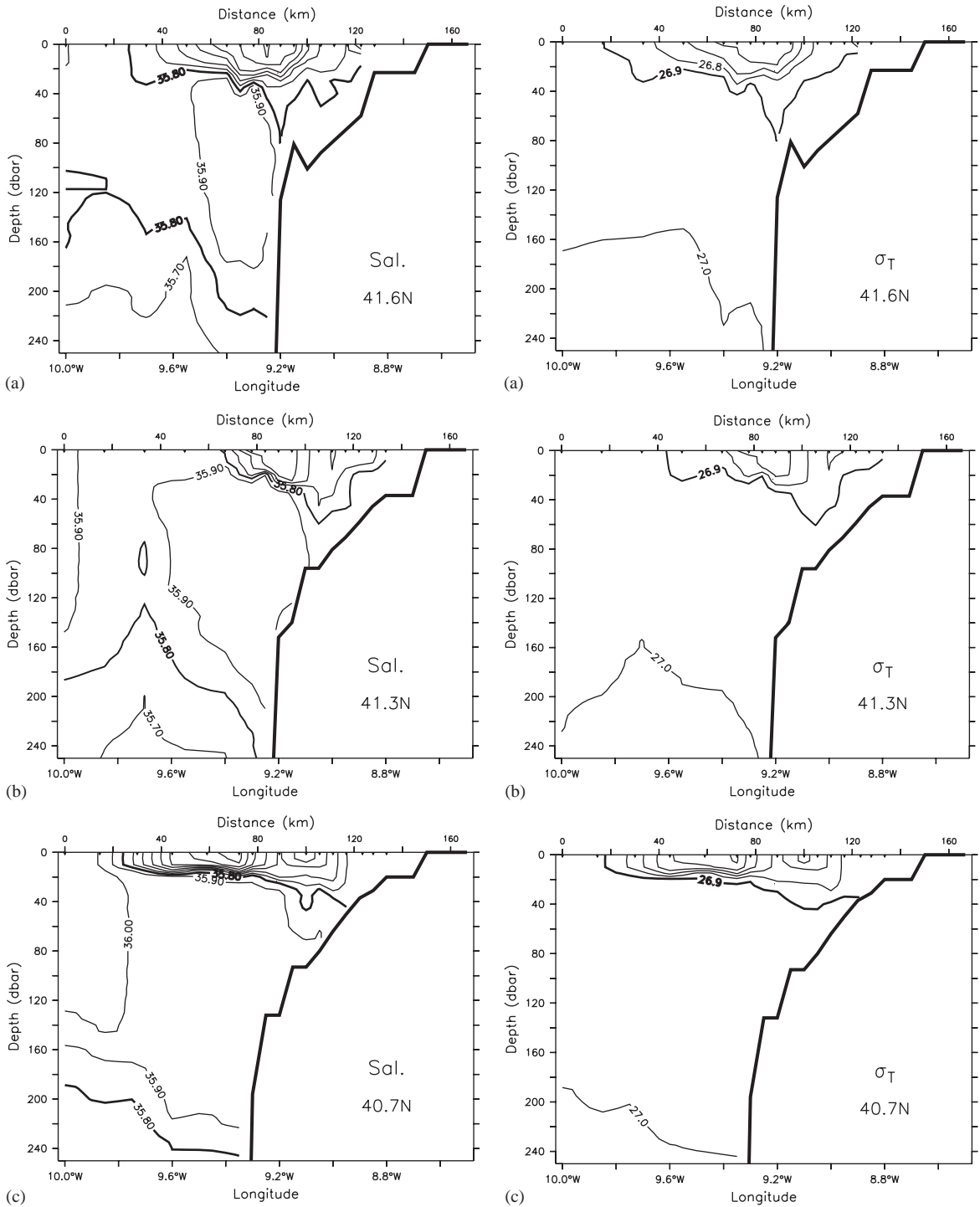


Fig. 7. Vertical fields of salinity (left) and density (σ_t ; right) for: (a) section V (41.6°N), (b) section IV (41.3°N), and (c) section II (40.7°N).

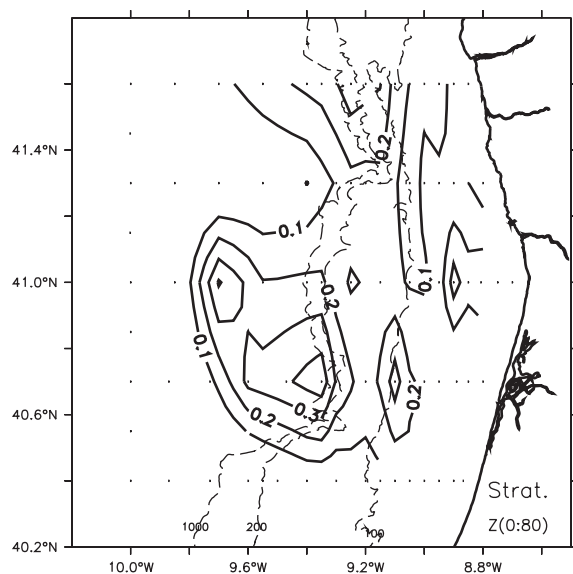


Fig. 8. Stratification of the 35.8 isohaline calculated as the density difference between the 5 m depth and the depth of the buoyant plume determined by the 35.8 isohaline surface.

along-slope flow. Along the slope and outer shelf the flow is northward and the transport inside the bottom Ekman layer is downslope. At the same time, over the shelf the flow is southward and the bottom layer transports water coastward. This divergence at the outer shelf is compensated by a downward mass flux with deepening of the isopycnals and the low salinity plume at that point (Fig. 7). The stratification in the temperature and salinity of the bottom layer over the outer shelf in sections III and V (Figs. 6a, b and 7a) may also be caused by the downslope transport associated with the poleward flow. This process could be responsible for the thickening of the plume, and also for it being trapped in that part of the shelf, thus constituting another constraint for offshore transport of the low salinity waters of the plume and all the biological material within it.

6. Ichthyoplankton distribution

The distribution of sardine eggs and larvae, as well as of all other fish eggs, is shown in Fig. 11.

Fish eggs were found mainly in the outer shelf with the highest concentrations over the shelf break (Fig. 11a). There is a clear association between the offshore distribution of the eggs and the area of influence of the buoyant plume (Figs. 4b and 8). The stations with most eggs over the shelf are also located in zones where the influence of the plume is more significant. As far as sardine eggs are concerned (Fig. 11b), they were mainly distributed over the shelf break, especially in the north, and only a small number were detected in the inner part of the shelf in the south. This indicates either an increased vulnerability of the sardine eggs to Ekman transport or that the spawning occurred at the outer shelf. However, sardine spawning is considered to be restricted to the continental shelf as observed from ichthyoplankton surveys (Ré et al., 1990) and from the distribution of adult fish (e.g., Dias et al., 1989; ICES, 2001). The adult distribution area rarely extends beyond the 100 m isobath. The occurrence of sardine eggs in the inner shelf in the south of the surveyed area (Fig. 11b) also suggests that spawning was mainly occurring over the continental shelf.

Fig. 11c shows the distribution of sardine larvae. There is not any significant difference in relation to the distribution of the eggs. However, it is clear that a considerable number of larvae were sampled at the shelf break in the southern part of the surveyed area.

However, the most interesting pattern is the spatial distribution of the mean length of the larvae presented in Fig. 11d, in which two patterns are identified: a meridional gradient in the mean length of larvae with the smaller ones mainly in the southern stations and the larger ones in the northern stations; and a cross-shore gradient with larger larvae found further offshore. Thus the observed distributions seem to indicate an offshore advection, especially in the southern part where the WIBP is observed to be spread further offshore (Fig. 4b), and also northward transport of the sardine larvae, with retention at the convergence zone. Note that the higher mean length of sardine larvae associated with northern stations is statistically significant as tested by one-way ANOVA (Table 1), as well as the inshore/offshore differences (Table 2).

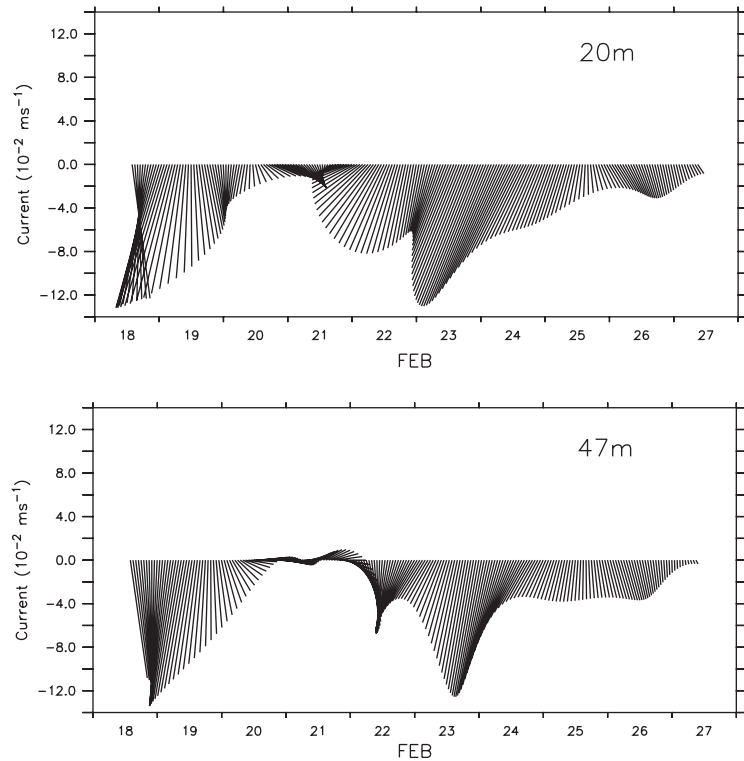


Fig. 9. Stick diagram of current meter measurements (cm/s; one stick every hour) at the mooring array located at the 80 m isobath (see Fig. 1 for location) from 18 to 27 February 2000: (a) current meter located at the 20 m depth level, and (b) current meter located at the 47 m depth level. Negative values correspond to equatorward currents.

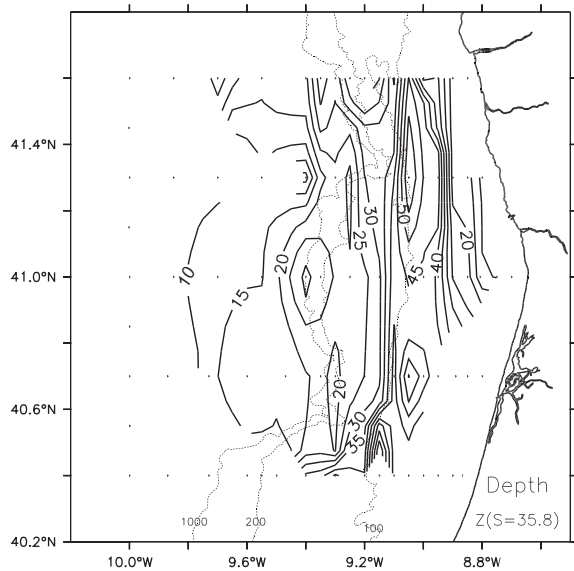


Fig. 10. Depth (m) of the 35.8 isohaline surface, which was considered representative of the lower boundary of the buoyant plume (WIBP).

7. A simple transport model

A time evolving surface flow field corresponding to the upwelling event from 18–22 February 2000 was estimated based on the information of the current meter data (Fig. 9), the calculated geostrophic currents (Fig. 3) and the wind-stress data (Fig. 2). The total surface velocity was calculated adding an Ekman layer velocity to the surface geostrophic flows beyond the 100 m depth zone and to the current meter derived velocities at the 100 m contour. The offshore velocity was estimated according to the expression:

$$\mathbf{v}_{\text{offshore}}(x, y, t) = \mathbf{v}_g(x, y) + \mathbf{v}_{\text{ek}}(t), \tag{1}$$

where \mathbf{v}_g stands for the calculated geostrophical velocities and \mathbf{v}_{ek} represents a time-evolving Ekman layer velocity.

Over the shelf the velocity was obtained by extrapolating the current meter time series at 47 m

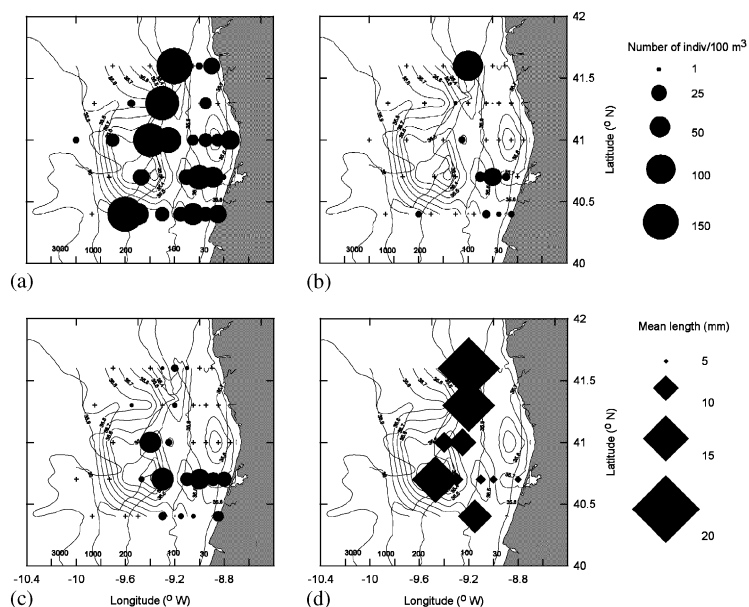


Fig. 11. Distribution and abundance of ichthyoplankton (0–50 m) superimposed on horizontal distribution (0–15 m) of salinity during February 2000: (a) number of fish eggs per 100 m^3 ; (b) number of sardine (*Sardina pilchardus*) eggs per 100 m^3 ; (c) number of sardine larvae per 100 m^3 ; and (d) mean length (mm) of sardine larvae. The thin lines represents the 30, 100, 200, 1000 and 3000 m bathymetry lines.

Table 1

Analysis of variance to test differences in the mean length of sardine larvae between northern (48–78) and southern (1–47) stations

Groups	Count	Sum	Average	Variance	
Southern stations	124	899.63	7.26	5.32	
Northern stations	18	316.63	17.59	12.29	
Source of variation	SS	df	MS	F	P-value
ANOVA					
Between groups	1679.06	1	1679.06	272.24	<0.001
Within groups	863.47	140	6.17		
Total	2542.53	141			

depth, which was considered representative of the interior velocity at the shelf, ($\mathbf{v}_c(t)$) throughout the shelf zone (although the differences are small in Fig. 9, the upper current meter (at 20 m) still shows some possible local influence of the plume):

$$\mathbf{v}_{\text{inshore}}(x, y, t) = \mathbf{v}_c(t) + \mathbf{v}_{\text{ek}}(t). \quad (2)$$

The choice of Eq. (1) or Eq. (2) was based on the local depth. The velocities in grid points shallower than 100 m were calculated with Eq. (2), and all the remaining velocity estimates were obtained with Eq. (1). The Ekman velocities were calculated using the expression $v_{\text{ek}} = \tau / (\rho df)$ (e.g., Cushman-Roisin, 1994), where ρ is the mean density, f the

Table 2

Analysis of variance to test differences in the mean length of sardine larvae between inshore (inside the 100 m isobath) and offshore (outside the 100 m isobath) stations

Groups	Count	Sum	Average	Variance	
Inshore stations	61	369.31	6.05	1.81	
Offshore stations	81	846.95	10.46	22.00	
Source of variation	SS	df	MS	F	P-value
ANOVA					
Between groups	674.23	1	674.23	50.52	<0.001
Within groups	1868.30	140	13.35		
Total	2542.53	141			

Coriolis parameter and d an estimate for the Ekman layer depth ($d = \sqrt{2\nu/f}$, where the eddy viscosity, $\nu = 10^{-2} \text{ m}^2/\text{s}$). Finally, τ is the surface stress calculated according to

$$(\tau_x, \tau_y) = \rho_a \cdot C_D \cdot |W|(w_x, w_y), \quad (3)$$

where ρ_a is the air density (1.22 kg/m^3), C_D is the drag coefficient (0.0012) and W the wind velocity (m/s). The resulting two-dimensional fields were interpolated into a regular grid with the same size as the sampled area and with a 1.1 km space resolution. All velocity estimates were interpolated to produce a time evolving velocity field with 6-h time steps over a period of 5 days (approximately 18–22 February 2002). The Lagrangian trajectories were calculated using a Runge–Kutta 2nd order scheme.

Groups of particles randomly distributed inside a 10 km radius were released at several locations over the shelf and were tracked along the domain during the 5 days (particles reaching the boundaries are retained there). The time step for tracking the particles was 5 min and the velocity fields were considered stationary between the velocity upgrades (each 6 h). Fig. 12 shows the paths of five groups of 30 particles each (in a total of 150) together with the initial (open circle) and final (star) position of the particles.

The particles were generally advected off the coast and to the south over the shelf. At the outer shelf, where the velocity transition occurs, it is possible to observe that the aggregation at the

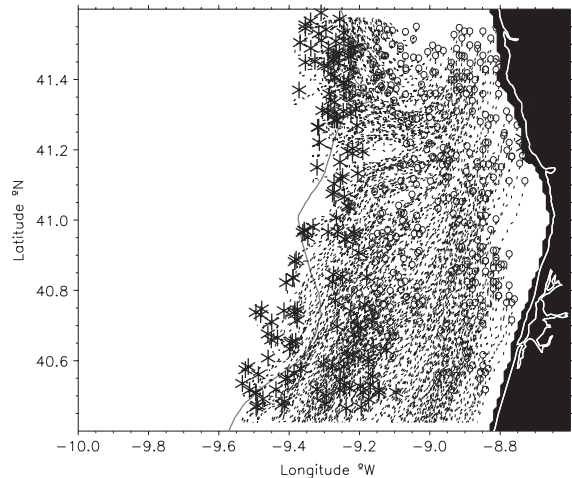


Fig. 12. Lagrangian model showing trajectory paths of particles between 18 and 22 February 2000, obtained with velocity estimates as described in the text. Circles represent the initial position and stars the final location. The solid line is the 200 m bathymetry line. Particles arriving to the meridional boundaries are artificially retained there by the model.

northern zone is different from the one in the south. In the former the particles were retained approximately at the shelf-break and drifted northward under the influence of the poleward flow. Note that a meridional strip of particles was formed. This strip is similar to the one observed in the ichthyoplankton distributions (e.g., Fig. 11a).

This simple simulation shows some important features of the transport but fails to capture the

role of the surface buoyant plume and convergence zone. The influence of the plume in the transport is only implicitly included in this simple model as far as it represents the surface velocity and the particles are always maintained at the surface. If the particles were allowed to migrate vertically they might leave the surface Ekman layer and thus be advected to the interior. However, the mixing inside the plume and the circulation associated with the density gradients are not included in this simple model.

Even with the simplifications used in this particle tracking Lagrangian model, the retention of the particles along the shelf-break is similar to the observed features. This retention is due to the role of the along-slope jet that acts as a barrier to the offshore Ekman transport. An outcome of the model is that the convergence band can be explained, at least partially, by these two circulation features once the processes related to the vertical circulation referred to before are excluded. It is also clear that there is a certain resemblance between the distribution of the particles in Fig. 12 and of the larvae in Figs. 11c and d; namely the offshore pattern in the southern part and in the convergence zone in the northern part. However, in the southern part of the domain a concentration of particles close to the slope is not evident, as in the case of fish eggs in Fig. 11a. Here, the influence of the plume may be decisive in retaining the material. However, as already stated, the model does not simulate the plume.

8. A mechanism for retention

The feature that retained most of the biological material, including the eggs and larvae of sardine and of other fish, was the convergence band located at the outer shelf.

A number of mechanisms may contribute to an explanation of the origin of the convergence band: (i) the strong along-slope component of the poleward flow; (ii) the vertical recirculation associated with the upwelling; and finally (iii) the dynamics of the bottom layer in the presence of an equatorward upwelling current over the shelf and poleward flow over the slope. All these mechan-

isms are a consequence of the joint effect of the poleward slope-flow (IPC) and of the presence of the low salinity plume (WIBP) during the upwelling event.

The plume essentially provides a vertical retention mechanism, whereas the poleward current acts horizontally, retaining most of the plume close to the slope and advecting it northward. In this process, a convergence zone is created where the plume is trapped and deepens, thus increasing the potential for retention. This process of retention is schematically presented in Figs. 13a and b.

Part of the plankton will probably return to the coast following the wind relaxation. However, the presence of the slope-flow may induce a return to a northern or to a southern zone depending on the sense of the advection at the slope and outer shelf. In fact, at the scale of several weeks or months the slope current may modulate this transport by introducing an along-slope component to the cross-slope component forced by the wind. Off Western Iberia the slope is essentially dominated by the presence of the IPC and it is expected that the resulting larval drift will be poleward as it was schematically represented in Fig. 13c. However, these hypotheses require further modelling efforts and observations.

9. Final discussion and conclusions

The results presented here provide indications that upwelling events during the spawning season of sardine could significantly change the distribution of their early life stages. The most significant features of the ichthyoplankton distributions are their accumulation along convergence zones, and their association with low-salinity surface distributions. In what concerns sardines, which are known to spawn over the shelf, the observed offshore distribution of their larvae (in particular older ones) may be interpreted as an indication of seaward transport.

Chícharo et al. (2003) observed that almost all sardine larvae caught during the survey are in good condition and only 0.64% were classified to be in a starving state. These results are even better than those obtained in other areas off the Iberian

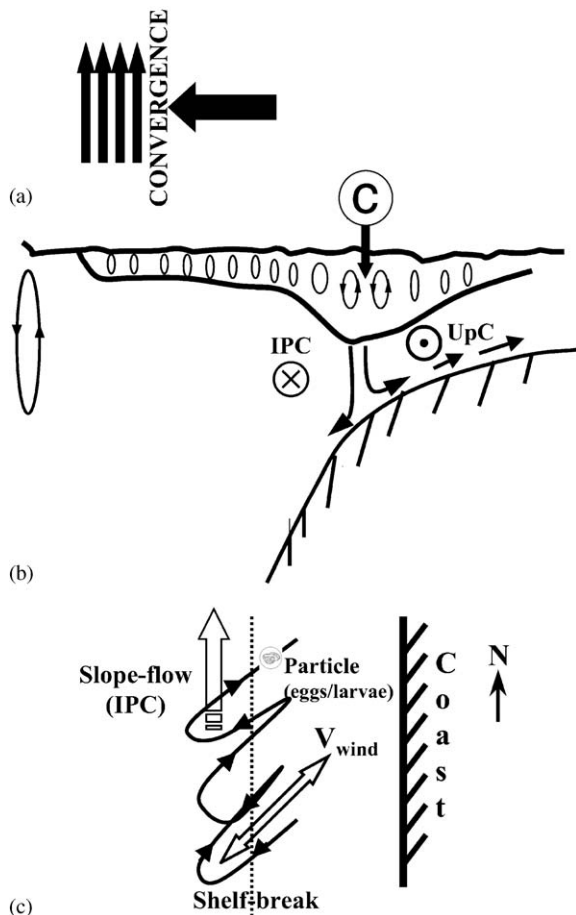


Fig. 13. Schematic representation of a retention mechanism and poleward egg and larval drift: (a) the convergence zone mechanism; (b) the vertical retention inside the buoyant plume (IPC—Iberian Poleward Current; UpC—Upwelling current; C—Convergence zone); and (c) the horizontal retention and modulated poleward transport due to the joint effect of the poleward slope flow (IPC) and the cross shelf Ekman transport (V_{wind}).

Peninsula during the spring (Chícharo, 1997; Chícharo et al., 1998). Despite the upwelling favourable winds, the offshore transport and survival of sardine larvae was constrained by other local features such as the Western Iberia Bouyant Plume (WIBP) and the Iberian Poleward Current (IPC); with the joint effect of both being the creation of conditions for retention of the larvae close to the shelf break.

In fact, the eggs and larvae were clearly associated with the low salinity pools and were probably advected inside them. In the process of offshore transport part of the larvae were also retained in the convergence zone. In both cases, the concentration of phytoplankton was relatively high (Figs. 4d and 6d), thus the larvae had access to a sufficient concentration of food to keep them in good nutritional condition. According to Govoni and Chester (1990), Grimes and Finucane (1991) and Sabatés et al. (2001) the plumes of continental fresh water are habitats that afford conditions favourable to the growth and survival of fish larvae.

The data indicate that older larvae (larger) tend to be advected northward along the convergence zone on the shelf break (Fig. 11d). In a previous work on the distribution of sardine larvae off the northern coasts of Spain, López-Jamar et al. (1995) also found the highest mean lengths off southern Galicia near the Portuguese border (about 42°N in the north of the present survey area) during March, and indicated that the prevailing surface current off northern Portugal during previous months was poleward.

These results suggest that in this area upwelling events might not have an immediate impact on the survival of sardine early life stages by reason of their transport offshore alone. However, the negative impact could be on longer time scales due to the combination of offshore advection and the presence of a shelf break/slope poleward current (Fig. 13c), which favours advection of sardine eggs and larvae from the spawning area, where other conditions could lead to poor survival conditions, such as strong upwelling off Galicia in the spring (e.g., López-Jamar et al., 1995).

The mechanisms reported herein may be found in other upwelling areas where slope flows and coastal buoyant discharge are important. This study indicates that the processes of larvae transport are strongly dependent on local features and cannot be treated with simplified Ekman models. In some cases, it can be far more complex. Within the same coastal upwelling region, different areas may exist where the transport patterns are specific and dependent on local aspects. The case of the Western Iberia Upwelling region is

illustrative, since both the poleward flow and especially the buoyant discharge are much increased in the northern part.

As these local factors can vary seasonally or interannually, significant fluctuations in the transport patterns are also introduced. In the case of Western Iberia, the buoyant discharge and poleward flow exhibit such variations. In years of strong poleward flow and an enlarged plume the negative impact of coastal upwelling on the transport is reduced. On the other hand, the absence of one or both of these factors will play the opposite effect contributing to interannual fluctuations.

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