Research papers

Composition and daytime vertical distribution of the ichthyoplankton assemblage in the Central Cantabrian Sea shelf, during summer: An Eulerian study

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A B S T R A C T

During summer, wind driven coastal upwelling dominates in the Central Cantabrian Sea (southern Bay of Biscay). Nevertheless, atmospheric forcing is highly variable and wind pulses may cause noticeable and fast hydrographic responses in the shelf region. In this paper, the composition and vertical distribution of the summer ichthyoplankton assemblage during the daytime at a fixed station, located on the Central Cantabrian Sea shelf, are documented. Also, the impact of a short-time scale hydrographic event on the abundance and structure of the larval fish assemblage is examined. Significant small-scale temporal hydrographic variability was observed. Currents showed changes in speed and direction and significant changes in thermocline depth were also observed. A total of 34 taxa of fish larvae were identified. *Engraulis encrasicolus* eggs and larvae of the shelf-dwelling species *Trachurus trachurus*, *Capros aper* and *E. encrasicolus* dominated the ichthyoplankton assemblage. The distribution of *E. encrasicolus* eggs and fish larvae was vertically structured. *E. encrasicolus* egg concentration increased exponentially towards the surface. Fish larvae showed a subsurface peak of concentration and their vertical distribution was not conditioned by thermocline depths. The short term hydrographic event did not affect the vertical distribution of fish larvae but it accounted for significant temporal changes in larval fish assemblage structure and abundance. Results suggest that temperature and light intensity are important factors in the vertical distribution of fish larvae. They also indicate that the temporal monitoring of the larval fish assemblage in this region requires multiple sampling sites.

1. Introduction

Fish eggs and larvae have heterogeneous vertical distributions (Heath, 1992). In stratified waters, the presence and position of the thermocline has been considered a major factor in the vertical distribution of fish larvae (Ahlstrom, 1959; Boehlert et al., 1985; Loeb, 1979; Röpke et al., 1993; Smith et al., 1999). Other studies, however, have found that vertical distributions are independent of the thermal stratification of the water column and related them with the vertical distribution of prey and larval behavior (Conway et al., 1997; Gray, 1996a; Gray and Kingsford, 2003; Leis, 1991; Olla and Davis, 1990; Röpke, 1993). It is well known that over the continental shelf, the water column shows a layered structure associated with current shear. So, the interaction between hydrodynamic processes and vertical distributions is pivotal in explaining horizontal distributions of fish larvae in shelf regions

(Govoni and Pietrafesa, 1994; John, 1985; John and Re, 1995; Smith and Suthers, 1999). It follows that the temporal variability of the larval fish assemblage at a fixed location would be related to the coupling between the vertical distribution of fish larvae and the hydrography of the region.

The shelf of the Central Cantabrian Sea (Southern Bay of Biscay) is narrow and the hydrography of the region is highly influenced by climatic factors. During autumn–early spring mixing period, the Iberian Poleward Current (IPC), which transports warm and saltier waters poleward along the shelf-break, reaches its maximum intensity (Peliz et al., 2003; Pingree and Le Cann, 1990). The intrusion of more saline waters into the Cantabrian Sea generates a sharp thermohaline shelf-slope front, which diminishes the across-shelf transport (Fernandez et al., 1993; Lavin et al., 2005). During summer, strong thermal stratification develops and north-easterly winds produce coastal upwelling (Botas et al., 1990; Wooster et al., 1976), also bordered offshore by a thermohaline front (Sanchez and Gil, 2000). The general surface current is then westward, transporting coastal upwelled water (Botas et al., 1990; Haynes and Barton, 1990). However,

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atmospheric forcing is highly variable and wind pulses may cause noticeable and fast hydrographic responses in the shelf, and shelf-slope regions (Gonzalez-Pola et al., 2005; Torres et al., 2003). In this context, it is instructive to examine whether and how these hydrographic events affect the larval fish assemblage structure in the region.

In this paper we describe the composition and the vertical distribution of the summer ichthyoplankton assemblage during the daytime at a fixed station, located in the central Cantabrian Sea shelf. Despite their importance, to our knowledge, there are no studies dealing with the vertical distribution of the ichthyoplankton assemblage in the region. We also examine the impact of a hydrographic event on the abundance and structure of the larval fish assemblage.

2. Materials and methods

The Perplan 0808 cruise took place in the second fortnight of August 2008 (Julian days 230–242), in the Central Cantabrian Sea shelf. An across-shelf transect of five stations, extending from the coast to the shelf-break, was sampled (Fig. 1). However, the sampling effort was concentrated on the Stn 2 of the transect (Fig. 1), and the five stations were occupied only on six of the eleven sampling days. Stn 2 was located around the middle shelf, at 14.2 km from the coast and over the 110 m isobath (Fig. 1).

2.1. Sampling procedure

Vertical profiles, down to 5 m above the bottom, of temperature, salinity and fluorescence were obtained at each station. Two SeaBird CTD probes were used. One CTD (a SBE 911), embedded within an oceanographic rosette, was used at stations in which water samples were required (stations 2 and 5). The other (a self-contained SBE 25) was used in the remainder stations and also when replicate ichthyoplankton hauls were made, or the meteorological conditions prevented us from using the rosette. Cross-checks between both CTDs showed strong agreement. Local winds and surface currents during the cruise were measured at the "Peñas" buoy, located over the slope at 43°43.80′N, 6°10.20′W, about 25 miles west of the

Fig. 1. Location of the study area, the sampling transect and the ODAS buoy 'Peñas' (★).

sampling section (Fig. 1) This buoy forms part of "the Deep Water Network" (DWN) ODAS buoy array, belonging to the Spanish Port Authority (Alvarez Fanjul et al., 2003).

Eulerian sampling for ichthyoplankton was conducted around midday, at the Stn 2 of the sampling transect. Sampling was carried out on 17 and daily from 20 to 29 August 2008. Sampling days were named as sampling Day 1 (sD01), 17 August, to sampling Day 11 (sD11), 29 August. Four replicate hauls were made on sD01 and three on sD02, sD06 and sD09. A multiple opening/closing net MultiNet MiDi, 50×50 cm^2 aperture (Multi-Net Hydro-Bios Apparatebau), equipped with 200 μm mesh nets, was used to collect zooplankton and ichthyoplankton at 5 depth strata (0–10, 10–30, 30–50, 50–75 and 75–100 m). Sampling strata were named as D1 (0–10 m) D2 (10–30 m), D3 (30–50 m), D4 (50–75 m) and D5 (75–100 m). The net was towed on oblique hauls, sampling from 100 m depth (10 m above the bottom) to the surface, at 2.5–3 knots (ship speed was continuously adjusted to maintain constant the wire angle) and at retrieval speed of 20 m per minute. The volume of water filtered in each stratum was measured by a flowmeter located in the mouth of the net. The mean volume of water filtered per haul was 131.7 m^3 (SE=23.3).

Zooplankton samples were preserved in a 5% solution of buffered formalin and seawater. In the laboratory, mesozooplankton individuals were counted using image analysis technique. A subsample from each sample was stained for 24 h with 0.2% eosin. The stained sample was scanned generating an image of 256 (eight-bit) colors, with a resolution of 1200 dpi. Images were processed using EBImage, an *R* (R Development Core Team, 2010) package. Each zooplankton individual was automatically counted and its length measured. When replicate hauls were available, only samples from a haul chosen at random were counted for zooplankton. Fish eggs and larvae from every sample were sorted and counted, under a binocular microscope. Only *Engraulis encrasicolus* and *Sardine pilchardus* eggs were identified. However, all larvae were identified to the lowest taxonomic level possible. Mesozooplankton (size fraction 0.2–2 mm) counts were standardized to no. of individuals per m^3. The number of *E. encrasicolus* eggs and fish larvae collected at each deep stratum was expressed as the number of individuals per 100 m^3. Also, the number of *E. encrasicolus* eggs and fish larvae collected at each haul was standardized to number per 100 m^3. Larvae (apart from those damaged) of the most abundant species *Trachurus trachurus*, *Capros aper*, *E. encrasicolus*, *Trachurus mediterraneus* and *Pagellus erhytrinus* were measured to the nearest 0.1 mm standard length using the ImageJ 1.44 p. image analysis software.

2.2. Data analysis

The average temperature profile for Stn 2 has been obtained. This was made by assembling a set of parameters resulting from breaking each individual temperature profile. These parameters, which describe the properties of the upper ocean layer structure, include the depth of the mixed layer, temperature in the mixed layer and shape and gradient of the seasonal thermocline. The profile calculated in this way preserves the water column structure (see Gonzalez-Pola et al., 2007, for further details).

To compare vertical distributions, weighted mean depths (WMD) of mesozooplankton, total fish larvae and taxa with ≥ 20 larvae were calculated for each haul as

$$\text{WMD} = \sum_{i=1}^{5} n_i d_i \bigg/ \sum_{i=1}^{5} n_i$$

where n_i is the concentration of individuals at ith stratum and d_i is the mid-depth of the ith stratum (Roe et al., 1984).
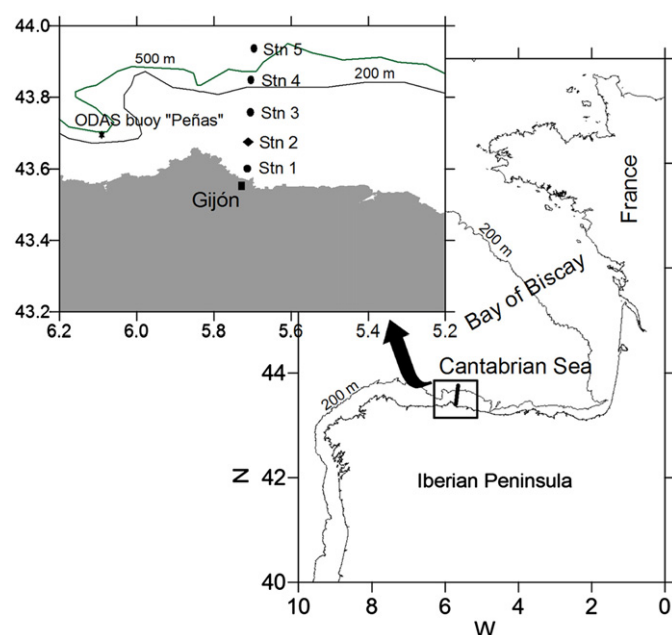
The relationship of the vertical distribution of fish larvae with the depth of maximum fluorescence and with the vertical distribution of zooplankton was examined using correlation analysis. We calculated the Pearson's correlation coefficient of WMDs of total fish larvae and larvae of most abundant taxa with the depth of maximum fluorescence and with WMDs of mesozooplankton. One-way ANOVA was used to determine if differences in the vertical distribution of fish larvae (differences in WMDs of total larvae and WMDs of larvae of dominant taxa) and larval abundance between the 4 replicate sampling days were significant. The inclusion of a taxon in the above analysis depended on its frequency and only included if it was present in enough hauls. Differences between the vertical distribution (differences in WMDs) of *T. trachurus* and *T. mediterraneus* were tested with Student's-*t* test for paired samples. One-way ANOVA was also used to test for significant differences in larval sizes of most abundant species between strata. Prior to analysis, data were tested for normality (Shapiro–Wilk test) and homogeneity of variance (Levene test) and $\log_{10}(x+1)$ transformed, if necessary. Student–Newman–Keuls (SNK) test was used to compare means when significant differences were detected by ANOVA (Zar, 1999). The limited number (even 0) of larvae caught at the two deepest strata limited our analysis on the vertical distribution of larval sizes to the 3 upper strata in the case of *C. aper*, *E. encrasicolus*, *T. mediterraneus* and *P. erhytrinus* and to the four upper strata in *T. trachurus*.

2.2.1. Vertical structure of the larval fish assemblage

Because differences in depth distribution of fish larvae between replicate days were not significant (see "Results" section), larval concentrations of each taxon and for each replicate day were averaged by depth stratum and included with single-day samplings in the study of the vertical structure of the larval fish assemblage. Larval concentrations for each taxon per depth stratum and per daily haul constituted a sampling unit (55) in the matrix used in the multivariate analysis.

Differences in larval fish assemblage structure among the 5 depth strata were explored with non-parametric ANOSIM. Cluster analysis in conjunction with non-metric multidimensional scaling (MDS) was used to identify depth and taxon assemblages. Only taxa (23) found in more than two sampling units were included in the analysis. Cluster analysis and MDS ordination were performed on a Bray–Curtis similarity matrix (Bray and Curtis, 1957), generated from the fourth root transformed larval fish concentrations at each sampling unit. Data were four root-transformed to down-weight the influence of dominant taxa. Sampling dendrograms were created using hierarchical, group-average clustering from the above Bray–Curtis similarity matrix. Dendrograms were cut to produce ecologically interpretable clusters. To verify our interpretation of the dendrograms, MDS ordination plots were generated from the same Bray–Curtis similarity matrix used in classification analysis. In both cases, a 2-dimensional ordination approach was adopted because stress levels (≤ 0.18) are considered sufficiently low when the combination of clustering and ordination analysis is used (Clarke, 1993; Clarke and Warwick, 2001).

2.2.2. Temporal variability of the larval fish assemblage

As with the study of the vertical structure of the larval fish assemblage, its temporal variability was explored with non-parametric ANOSIM. With this test we assessed differences in larval fish assemblage structure among the 4 replicate days. Cluster analysis in conjunction with non-metric multidimensional scaling (MDS) was used to identify larval fish assemblages. With the similarity percentages routine (SIMPER), we identified species characteristic of each larval fish assemblage depicted by classification and ordination. Only taxa found in more than two hauls (21) were included in the analysis. As above, multivariate analysis was performed on a Bray–Curtis similarity matrix, generated from the fourth root transformed larval fish concentrations at each haul.

Univariate analyses were carried out with STATISTICA (StatSoft, 2005) and IBM SPSS version 19 for Windows, while multivariate analyses were performed with PRIMER 6.1.6 (Clarke and Warwick, 2001) statistical packages.

3. Results

3.1. Hydrography

Summer 2008 was atypical as several westerly wind pulses affected the region (Fig. 2a), however dominant surface currents, as observed by the ODAS "Peñas" buoy, were westwards (Fig. 2b). The start of the Perplan 0808 cruise was characterized by the passage of a low-pressure system through the north of the Iberian Peninsula producing unusual, for this time of the year, strong westerly winds along the Cantabrian Sea. Westerly wind pulses
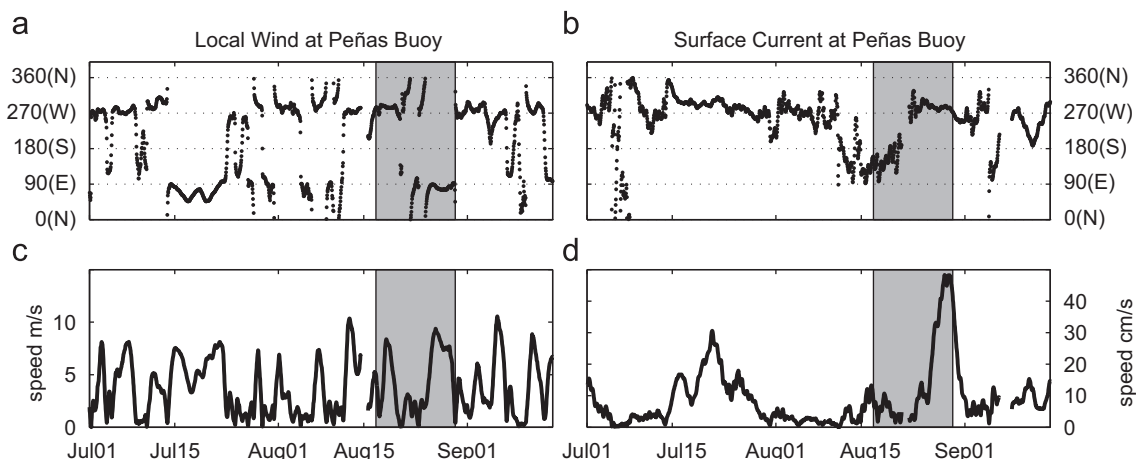

Fig. 2. Upper panel: (a) wind direction and (b) speed. Bottom panel: (c) surface current direction and (d) current speed measured at the Cape Peñas buoy. Following the established conventions, wind direction is that of origin while current direction is that of advance. The sampling period is indicated in gray. Series have been low passed (with a 30 h cut-off period Godin boxcar filter).

on 12–13 and on 18–19 August (Fig. 2a and c) altered the summer hydrographic conditions of dominant coastal upwelling (westward currents) producing a surface, south-eastward current pulse (Fig. 2b and d). From 20 to 29 August (sD02–sD11), conditions progressively returned to a summer-like situation, with north-easterly winds. Westward surface currents reached the strongest values by the end of the cruise (Fig. 2b and d).

The hydrographic structure along the sampled section changed accordingly to the wind regime shift. Fig. 3 shows the hydrographic sections on sD03, sD08 and sD11, when the five stations of the transect were sampled. There are no direct measurements of currents along the section but geostrophic flow fields can be inferred from density sections (Fig. 3c). It can also be observed in Fig. 3 that the overall density field is almost fully modulated by the temperature field. Salinity (Fig. 3b) is only of interest as tracer of water origin. On sD03, downwelling conditions were evident with isotherms and isopycnals sinking towards the coast (Fig. 3a and c). There was also a jet-like structure at the shelf-break, evidenced by the uplifting of the isothermals and isopycnals in this region (Fig. 3a and c). A patch of saline water was found at the surface, just above the shelf-break

(Fig. 3b). On sD08, the thermocline had begun to re-stratify and upwelling conditions dominated at the inner shelf, but conditions at the shelf-break were still of transition (Fig. 3a). By sD11, the upwelling was fully developed with uplifting of isotherms close to the coast (Fig. 3a). The doming of the isopycnals to both, the jet-like structure (sD03) and the fully developed upwelling (sD11), implies geostrophic velocity anomalies of around 15–20 cm per s^{-1}. Fluorescence sections (Fig. 3d) showed a subsurface chlorophyll maximum layer.

The sequence of temperature profiles shows significant changes in thermocline depths (Fig. 4, upper panel). Thermocline evolved from intermediate depths at the beginning of the cruise to the greatest depth around the middle of the cruise, reaching the shallowest depths at the end of the cruise, under upwelling conditions. At the same time, temperature of the mixed layer increased from ~ 19 to $> 21\,^{\circ}$C. The average thermocline depth for the whole sampling period was 52.9 m. Fluorescence profiles, in accordance with fluorescence sections (Fig. 3d), consistently showed a deep chlorophyll maximum (DCM), located close to the thermocline (Fig. 4, bottom panel).
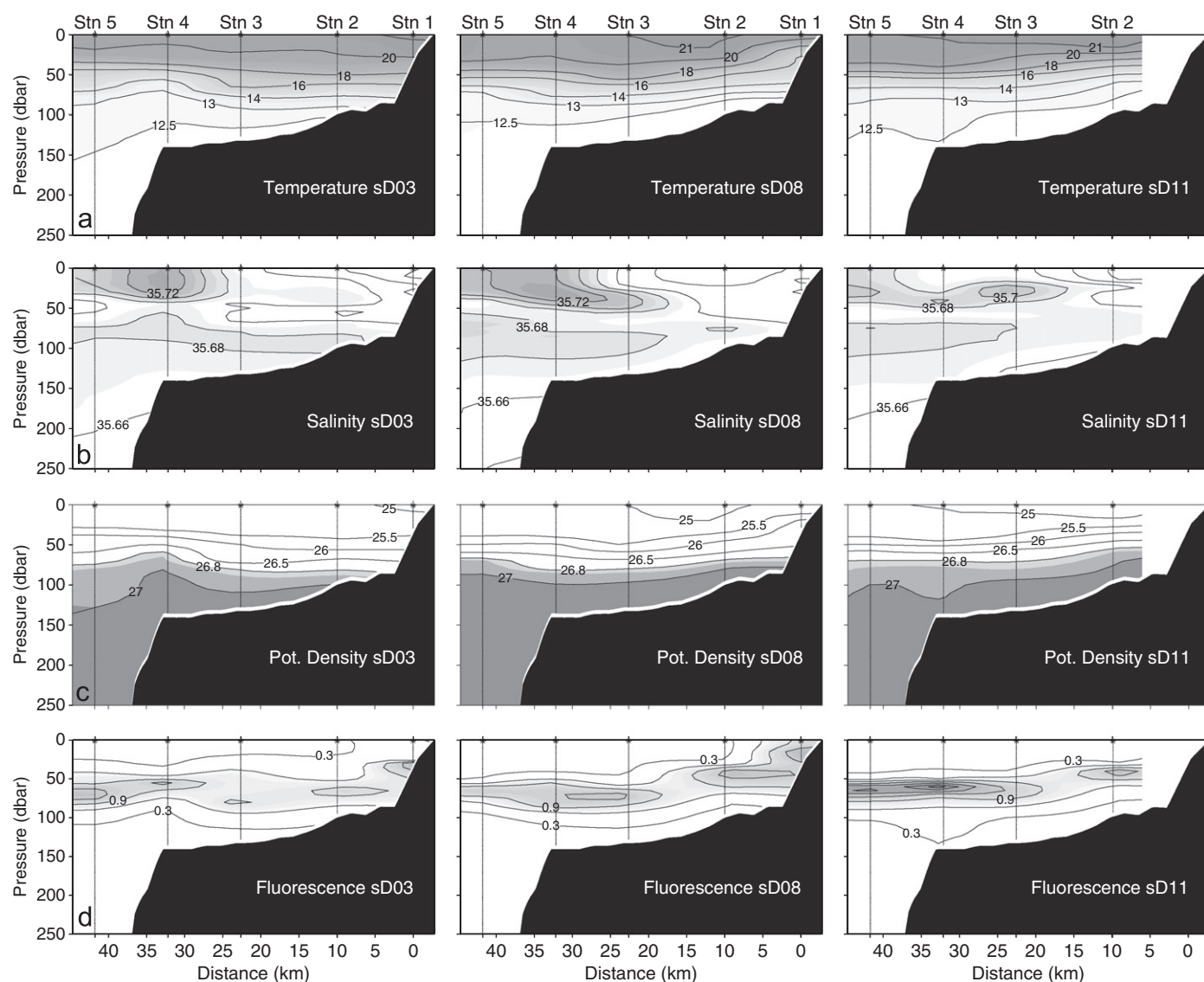

Fig. 3. Cross-shelf sections of (a) temperature, (b) salinity, (c) potential density and (d) fluorescence on 21 (sampling Day 3), 26 (sampling Day 8) and 29 (sampling Day 11) August 2008.
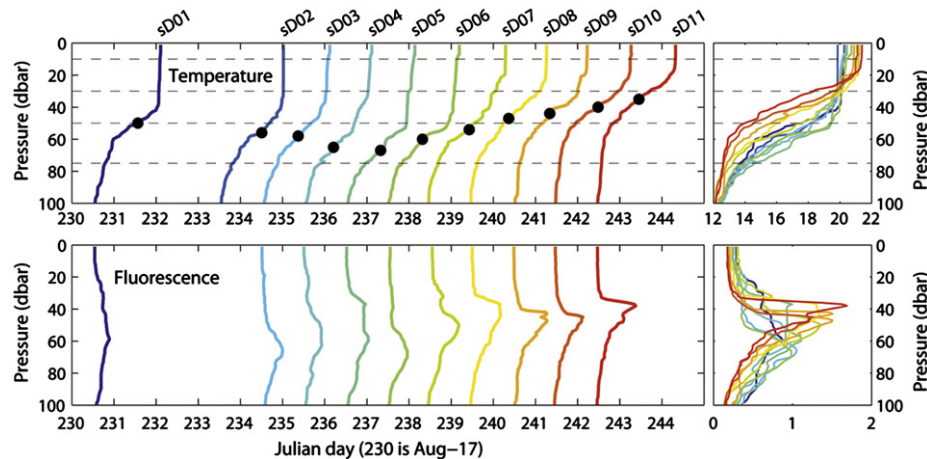
Fig. 4. Time series profiles of temperature (upper panel) and fluorescence (bottom panel). Sampling strata are depicted (dashed lines) in the upper panel (the bottom of the deepest stratum coincides with the bottom X-axis). Thermocline depth (●) over each temperature profile is also indicated in the upper panel.

3.2. Taxonomic composition and abundance of the ichthyoplankton assemblage

E. encrasicolus eggs accounted for 57.3% of the total fish egg concentration. Only one S. pilchardus egg was collected. The rest remained unidentified.

A total of 34 taxa (28 species, 3 genus and 3 families) of fish larvae from 21 families were identified (Table 1). The larval fish assemblage was widely dominated by larvae of neritic (shelf-dwelling) species. Only two species, Ceratoscopelus maderensis and Maurolicus muelleri (representing 0.15% of the total larval concentration), belonged to the oceanic mesopelagic habitat. The most abundant species were T. trachurus, C. aper and E. encrasicolus that accounted for 52.2% of the total larval fish concentration. Concentrations of other 16 taxa were $> 1\%$ of the total, while concentrations of 15 taxa were $< 1\%$ (Table 1).

3.3. Vertical distributions and vertical structure of the larval fish assemblage

Zooplankton showed similar and higher concentrations in the three upper strata, the region of the thermocline and mixed layer, than in the two deepest strata (Fig. 5a). E. encrasicolus eggs showed a relatively wide vertical distribution, with concentrations increasing exponentially towards the surface (Fig. 5b).

Differences in WMDs of total larvae and WMDs of larvae of dominant taxa between the 4 replicate days were not significant (ANOVA; $p > 0.05$, in all cases). This similarity in depth distribution of fish larvae justifies combining all hauls for each taxon to give a description of their overall patterns of vertical distribution.

The distribution of total fish larvae was vertically structured showing a subsurface peak of concentration (Fig. 5c). Larval fish taxa showed two general patterns of vertical distribution. One group included species with WMDs located above the thermocline. Within this group some taxa, species listed in Fig. 5, from C. aper (Fig. 5d) to T. mediterraneus (Fig. 5l), showed a shallow distribution (WMDs < 31.0 m), with very few or even with no larvae in the two deepest strata. For some others, T. trachurus, Arnoglossus spp and Cepola rubescens, their larvae were distributed through the whole water column (Fig. 5m, n and o, respectively). The other group, much less numerous, was formed by taxa with deeper distribution, with WMDs located below the thermocline. Within this group, Pomatoschistus marmoratus, Pomatoschistus microps and Pomatoschistus minutus (Fig. 5p, q and r, respectively) showed a wider vertical distribution, while

Callionymus spp and Merlucius merlucius were restricted to the three deeper strata (Fig. 5s and t, respectively). It should be underlined that T. mediterraneus showed a significant shallower distribution, WMD=20.2 m, than its congeneric species T. trachurus, WMD=35.8 m (Student's-t test for paired samples, $p < 0.01$). The different vertical distributions of both species are also apparent in Fig. 5l and m.

Correlations of vertical distribution of fish larvae with depth of chlorophyll maximum and with the vertical distribution of zooplankton are shown in Table 2. The only significant correlation found was between the vertical distribution of E. encrasicolus larvae and mesozooplankton.

The number of larvae measured per species, the size parameters (mean, minimum and maximum size), the mean size of larvae per depth stratum and the results of the ANOVA and SNK tests are shown in Table 3. All species showed relatively small sized larvae with quite homogeneous vertical distribution. Only T. trachurus and P. erhytrinus showed significant differences in larval sizes between strata. Larvae of T. trachurus were larger at the deepest stratum while larvae of P. erhytrinus increased their size towards the surface (Table 3).

The ANOSIM test ($R=0.35$, $p < 0.01$) showed significant differences in the vertical structure of the larval fish assemblage. Cluster analysis identified 2 major groups (a surface and a deep) of sampling units, at a similarity level of 30% (Fig. 6a). The surface group included almost only sampling units from D1, D2 and D3, mainly located above the thermocline (Fig. 4 upper panel). While, the deep group included sampling units from D4 and D5, mainly located below the thermocline (Fig. 4 upper panel). The MDS ordination plot (Fig. 6b) showed similar grouping to cluster analysis, with surface sampling units located on the right side of the plot and deeper sampling units on the left. This two-group classification was reinforced by the formation of a surface and a deep taxon assemblages, defined by cluster analysis (Fig. 7a) and MDS ordination (Fig. 7b). The surface assemblage, much more diverse, included those taxa with WMDs located above the thermocline, while the deep assemblage included taxa with WMDs located below the thermocline.

3.4. Temporal variability

Differences in larval concentrations between the 4 replicate days were significant for total larvae and for E. encrasicolus and T. trachurus (ANOVA, $p < 0.01$ in all cases). Total larval abundance decreased from sD01 to sD02. From sD02, abundance increased

Table 1

Taxon list, mean concentration and percentage of total concentration for all fish larvae collected.

Taxon	Mean concentration (no. 100 m^{-3})	Total concentration (%)
Family Blennidae		
Parablennius pilicornis	0.08	0.13
Family Bothidae		
Arnoglossus laterna	0.39	0.58
Arnoglossus spp	1.59	2.37
Family Callionymidae		
Callionymus spp	1.34	2.01
Family Carangidae		
Trachurus mediterraneus	5.36	8.01
Trachurus trachurus	14.40	21.57
Family Carapidae		
Echiodon drummondi	0.05	0.07
Family Caproidae		
Capros aper	12.81	19.13
Family Cepolidae		
Cepola rubescens	2.17	3.24
Family Clupeidae		
Sardina pilchardus	0.04	0.06
Family Engraulidae		
Engraulis encrasicolus	7.64	11.42
Family Gobiidae		
Lebetus guilleti	0.29	0.41
Pomatoschistus marmoratus	1.52	2.27
Pomatoschistus microps	1.57	2.34
Pomatoschistus minutus	1.55	2.32
Pomatochistus pictus	0.07	0.10
Unidentified spp	0.77	1.15
Family Labridae		
Coris julis	0.18	0.27
Family Merlucciidae		
Merluccius merluccius	0.76	1.13
Family Mugilidae		
Mugil cephalus	1.96	2.92
Family Myctophidae		
Ceratoscopelus maderensis	0.03	0.04
Family Ophidiidae		
Ophidion barbatum	0.07	0.11
Family Scorpaenidae		
Scorpaena porcus	0.41	0.62
Family Serranidae		
Serranus cabrilla	1.41	2.10
Family Sparidae		
Diplodus spp	0.12	0.17
Oblada melanura	0.04	0.07
Pagellus acarne	0.86	1.28
Pagellus bogaraveo	1.67	2.49
Pagellus erythrinus	4.17	6.22
Pagrus pagrus	0.21	0.31
Unidentified spp	0.13	0.20
Family Sternoptychidae		
Maurolicus muelleri	0.08	0.11
Family Trachinidae		
Trachinus draco	1.39	2.07
Family Triglidae		
Unidentified spp	0.05	0.07
Unidentified larvae	1.77	2.65

(Fig. 8). *E. encrasicolus* larval abundance was lower on samplings days 1 and 2 than on sD06 and sD09 (Fig. 8). As for *T. trachurus*, its larval abundance did not follow a defined pattern (Fig. 8).

Post-hoc analysis showed that total larval abundance was significantly higher on sD09 than on sD02 (Tukey test, $p < 0.05$). *E. encrasicolus* abundance was significantly higher on sD06 and sD09 than on sD01 and sD02 (Tukey test, $p < 0.01$, in both cases). For *T. trachurus*, larval abundances were similar between sD01 and sD06 and between sD02 and sD09 (Tukey test, $p > 0.05$). Abundances on sD01 and sD06 were significantly lower than on sD02 and sD09 (Tukey test, $p < 0.01$, in both cases).

The ANOSIM test ($R = 0.63$, $p < 0.01$) showed significant differences in larval fish assemblage structure among the 4 replicate days. Cluster analysis separated the 4 replicate days into two groups at a similarity level of 56% (Fig. 9a). One of the groups (Gr. 1) included hauls from sD01, sD06 and sD09, while the other (Gr. 2) included hauls from sD02 (Fig. 9a). MDS ordination produced the same picture with replicates from sD02 located on the right side of the MDS plot and replicates from the other sampling days located on the left (Fig. 9b). Taxa that typified each group, as identified by SIMPER analysis, are listed in Table 4. The most outstanding difference between the two groups is the comparatively low contribution of taxa with shallow distribution (Table 4, Fig. 5) to the average similarity within the Gr. 2.

4. Discussion

4.1. Hydrography

The hydrographic situation in the southern Bay of Biscay by late August tends to be quite stable. Nevertheless, during August 2008 strong westerly wind pulses before and at the beginning of the cruise altered the summer coastal upwelling conditions in the area, producing a well-developed downwelling pulse. The meteorological event at the beginning of the cruise produced a response in the dynamics and in the hydrographic structure of the water column on the continental shelf. Surface currents and thermocline depth changed accordingly. The salinity of the water patch, found over the shelf-break, was within the range of subtropical saltier waters associated with the IPC (Frouin et al., 1990; Rios et al., 1992) and indicates water advection from the west, a typical winter situation. As the cruise progressed, hydrodynamic conditions progressively reverted to coastal upwelling. The above sequence of events provides a very interesting scenario to study the response of the larval fish assemblage at a fixed location to such an environmental perturbation.

4.2. Composition and abundance of the ichthyoplankton assemblage

E. encrasicolus eggs showed higher abundances than previously found for this species in a time-series study (July 2001–June 2004) including our sampling station (Rodriguez, 2008). The larval fish assemblage, dominated by *T. trachurus* and summer spawning species, was broadly similar to that found in the region, in August of the above mentioned years (Rodriguez, 2008). The difference lies in the higher abundance recorded for *E. encrasicolus* larvae (3rd in abundance) in this study, in comparison with August 2001–2003 (Rodriguez, 2008). Relatively high *E. encrasicolus* egg and larval abundance were also recorded during August 2007. Nevertheless, abundance decreased again in 2009 to similar values recorded in the period 2001–2006 (Rodriguez, unpublished data). The relatively high *E. encrasicolus* larval abundance recorded in some years in our study area could be related to the westward occasional extension of the main spawning area of this species in the southern Bay of Biscay, located in the eastern Cantabrian sea shelf (Motos et al., 1996), The salinity front (saline patch) and the jet-like structure found at the beginning of
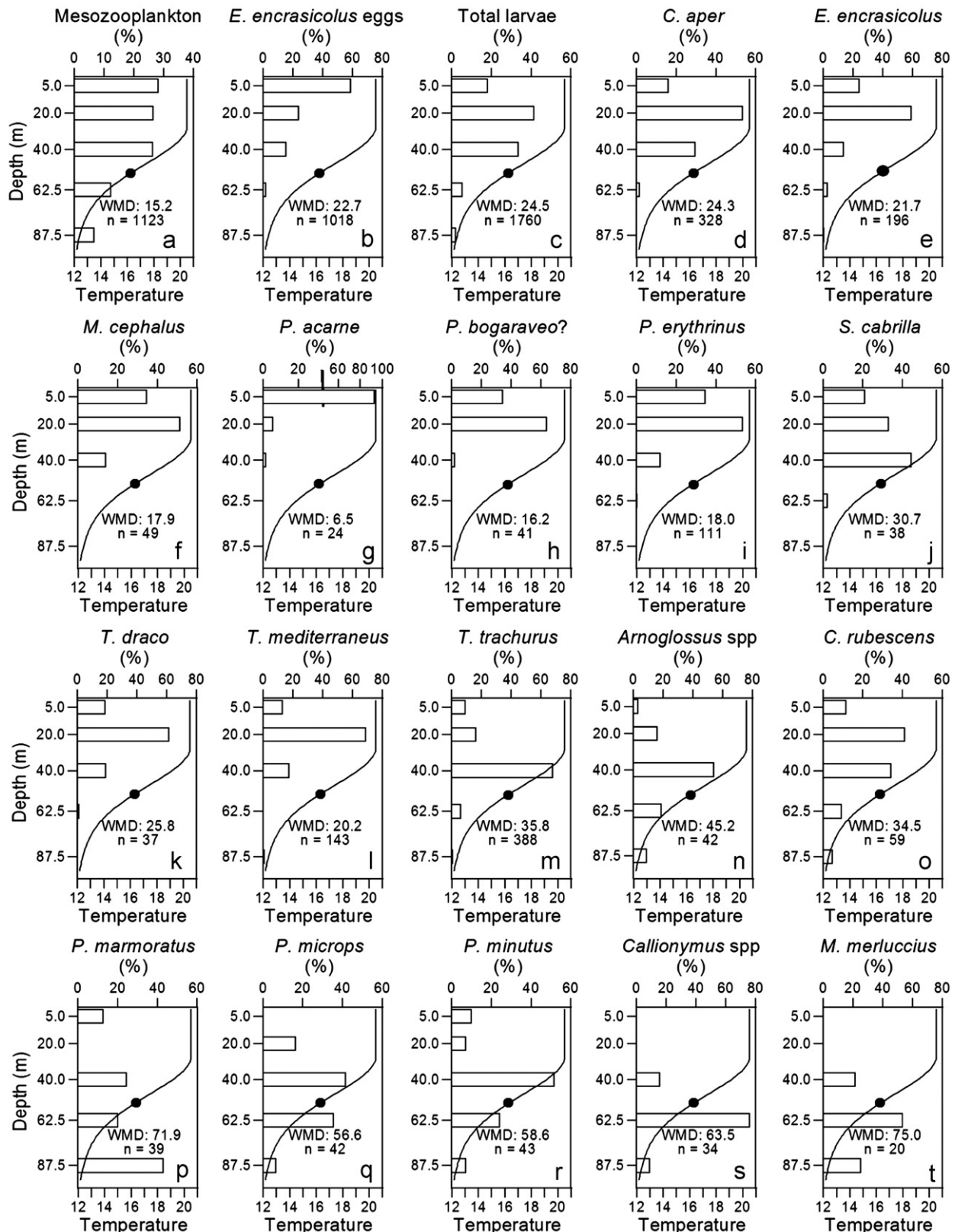
Fig. 5. Vertical distribution of mesozooplankton, *Engraulis encrasicolus* eggs, total larvae and larvae of dominant taxa. Percentages are based on the mean abundance at all sampling days for each depth stratum. Note the different scale of upper *X*-axis. *Y*-axis labels are the mean depth for each sampling stratum. The average temperature profile is included and the average thermocline dept indicated on it. Also, the weighted mean depth (WMD) and the number of *E. encrasicolus* eggs and larvae of each taxon are shown.

the cruise, under downwelling conditions, and the reported density front associated with coastal upwelling (Sanchez and Gil, 2000) may account for the low concentration recorded for larvae of oceanic mesopelagic species. These structures would function as a barrier preventing oceanic larvae from coming into the shelf.

4.3. Vertical distributions and vertical structure of the larval fish assemblage

The pattern of vertical distribution shown by anchovy eggs, relatively wide and with abundances increasing exponentially towards the surface is consistent with that predicted by the model proposed Boyra et al. (2003) for the vertical distribution of anchovy eggs, under a scenario of high salinity and turbulence. Salinity was considered to be high because it was above of 34, the threshold salinity used by Boyra et al. (2003) to distinguish between low and high salinity waters. Also, the relatively high wind speeds recorded during most of the cruise (Fig. 2c) suggest relatively high turbulence, reflected in the relatively deep (average 28.3 m) surface mixed layer. In any case, the occurrence of *E. encrasicolus* eggs, in the upper surface layers of the water column, above the thermocline, with the highest abundance recorded in the upper sampled stratum (0–10 m depth), is consistent with that reported for this species in the Mediterranean Sea (Olivar and Sabates, 1997; Palomera, 1991), in the Adriatic Sea (Coombs et al., 2003) or in the Bay of Biscay (Coombs et al., 2004; Motos and Coombs, 2000). To explain the wider vertical distribution found in our study compared to previous studies, the spawning location of *E. encrasicolus* in the water column and egg behavior should also be considered. *E. encrasicolus* spawning occurs predominately in the mixed layer, above the thermocline, in the top few meters of the water column (Coombs et al., 2004; Olivar et al., 2001), between 19:00 and 06:00 h, peaking around midnight (Garcia and Palomera, 1996; Motos, 1996). Also, according to Motos and Coombs (2000) and Coombs et al. (2004), *E. encrasicolus* eggs tend to sink as they develop. For a temperature of 20.04 °C, similar to that of the mixed layer in our study, the egg development time has been calculated to be about 42 h (Regner, 1985). So, at the time of our sampling, around midday, we would be collecting *E. encrasicolus* eggs at their mid and advanced development stages, with the consequent deeper distribution. Eggs sinking would be favored by the relatively deep surface mixed layer, resulting in a wider vertical distribution of *E. encrasicolus* eggs.

The distribution of fish larvae, vertically structured, is consistent with that reported in coastal-shelf waters during the daytime (e.g. Brewer and Kleppel, 1986; Gray, 1996a, 1998; Haldorson et al., 1993; Leis, 1991). The segregation of the larval fish assemblage based on the position of the thermocline with a surface assemblage, located above, and a deep assemblage, located below has already been reported (e.g. Ahlstrom, 1959; Kendall and Naplin, 1981). Nevertheless, the influence of the thermocline on the vertical distribution of fish larvae has been questioned (Conway et al., 1997; Gray, 1996a; Gray and Kingsford, 2003; Olivar and Sabates, 1997; Southward and Barret, 1983). The similarity in depth distribution of fish larvae between the 4 replicate days, with a quite different vertical structure of the water column, indicates that the vertical distribution of fish larvae was not conditioned by the thermocline position. It also indicates that the vertical distribution of fish larvae was not altered by the hydrographic event affecting the region at the beginning of the study, on 18 and 19 August. Other studies have suggested that prey distribution and larval behavior are more important than thermocline (Gray, 1996a; Olla and Davis, 1990; Röpke, 1993; Southward and Barret, 1983). The positive correlation coefficients, although not significant, found between the vertical distribution of fish larvae and DCM (Table 3) would suggest some relationship between the vertical distribution of fish larvae and the vertical distribution of their prey. DCM may constitute an important feeding region for fish larvae because copepod nauplii and copepodites, main food items for fish larvae, would concentrate there (Hunter, 1981; Olivar et al., 2001; Sabates et al., 2008; Smith and Suthers, 1999). In the same way, the negative correlation found between the vertical distribution of fish larvae and mesozooplankton (Table 3) would indicate vertical segregation between both planktonic components. This could be the result of competition for food, as mesozooplankton also feeds on microzooplankton (Batten et al., 2001; Wu et al., 2010).

In this study, species that showed the shallowest distribution reproduce during the warmer months in the region, while species that showed a wider or a deeper vertical distribution reproduce, either all year round, e.g. *T. trachurus*, or have an extended period of reproduction that includes colder seasons, e.g. *Arnoglossus* spp, *Merluccius merluccius* and *P. microps* (Froese and Pauly, 2010; Hureau, 1996; Rodriguez, 2008). This would indicate preference for warmer, surface waters by larvae of summer spawning species while larvae of species that also reproduce in colder seasons have a wider vertical distribution (e.g. *T. trachurus*, *C. rubescens*) and even show preference for colder, deeper waters (e.g. *Callionymus* spp and *M. merluccius*). The preference for warmer waters by species that reproduce during the warmer months is supported by the significant shallower distribution of the summer spawning *T. mediterraneus* against its congeneric species *T. trachurus*, which

Table 2
Correlation coefficients between weighted mean depth (WMD) of larvae of most abundant taxa with depth of chlorophyll maximum (DCM) and WMD of mesozooplankton (Mesozoop.).

WMD	DCM	Mesozoop.
Total larvae	0.12	− 0.16
Capros aper	0.07	− 0.42
Engraulis encrasicolus	0.16	− 0.63*
Pagellus erythrinus	0.23	− 0.24
Trachurus trachurus	0.19	− 0.03

* $p < 0.05$.

Table 3
No. of larvae measured, mean larval size per depth stratum and results of ANOVA and post-hoc SNK test examining differences in larval size between depth strata (n/a: data not available; ns: not significant).

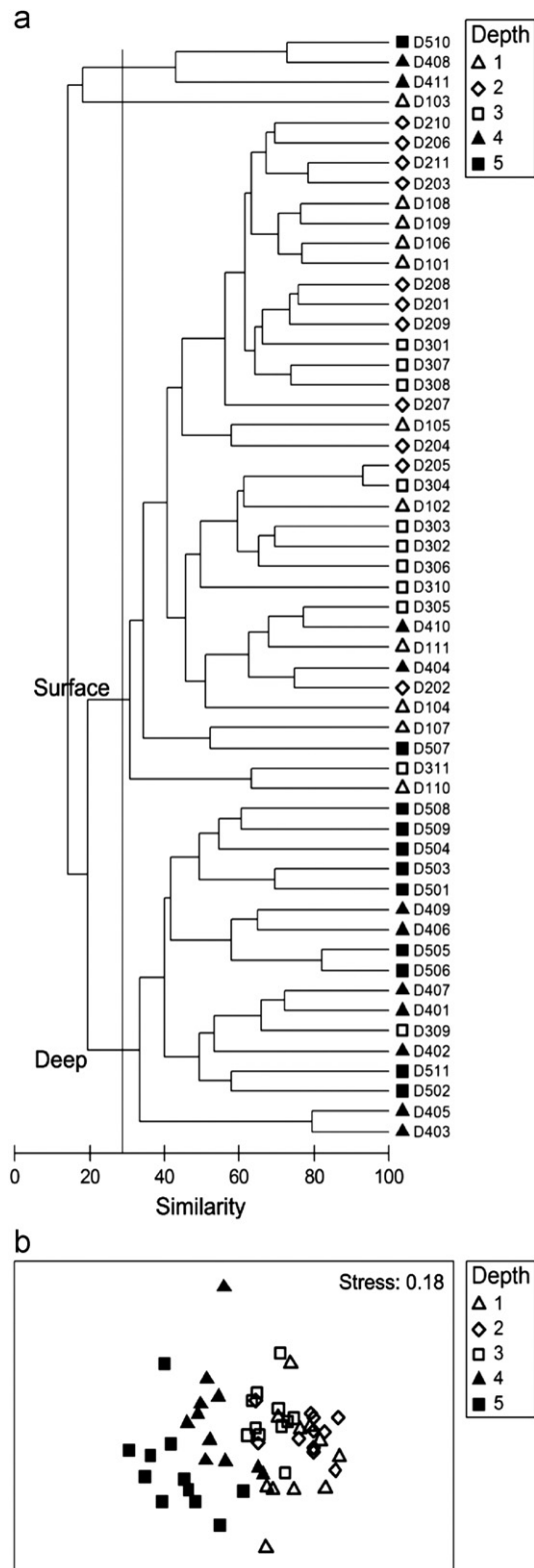| Species	No. of larvae measured and size parameters				Mean larval size per depth stratum				ANOVA	
	No.	Mean	Min	Max	D1	D2	D3	D4	F	P
Trachurus trachurus	311	2.8	1.5	6.3	2.7	2.5	2.7	3.6	9.27	< 0.01
Capros aper	268	2.1	1.1	4.0	2.1	2.1	2.1	n/a	0.25	ns
Engraulis encrasicolus	160	3.9	2.2	16.9	4.6	3.7	3.9	n/a	1.22	ns
T. mediterraneus	115	2.8	1.6	4.7	2.8	2.7	3.1	n/a	3.37	ns
Pagellus erhytrinus	95	2.7	1.8	4.5	3.1	2.7	2.3	n/a	7.87	0.01
SNK test										
T. trachurus	D1=D2=D3 < D4									
P. erhytrinus	D1 > D2 > D3									

Fig. 6. (a) Sampling units dendrogram resulting from the cluster analysis performed on a Bray–Curtis similarity matrix generated from the four root transformed larval fish concentrations at each sampling unit. The two identified clusters, separated at 30% similarity threshold, are indicated. Sampling codes are the following: left figure for depth stratum and right two figures for sampling day. (b) Two-dimensional MDS plot generated from the same similarity matrix as (a).

Fig. 7. (a) Taxon dendrogram resulting from the cluster analysis and (b) two-dimensional MDS plot generated from the same similarity matrix as Fig. 6. The two identified clusters, formed at 18% similarity threshold, are indicated in (a).

Fig. 8. Temporal evolution of larval fish concentrations of total larvae and larvae of *T. trachurus* and *E. encrasicolus*.

reproduces all year round. All this suggests temperature selection by taxon. As consequence, this could be a main factor in the vertical distribution of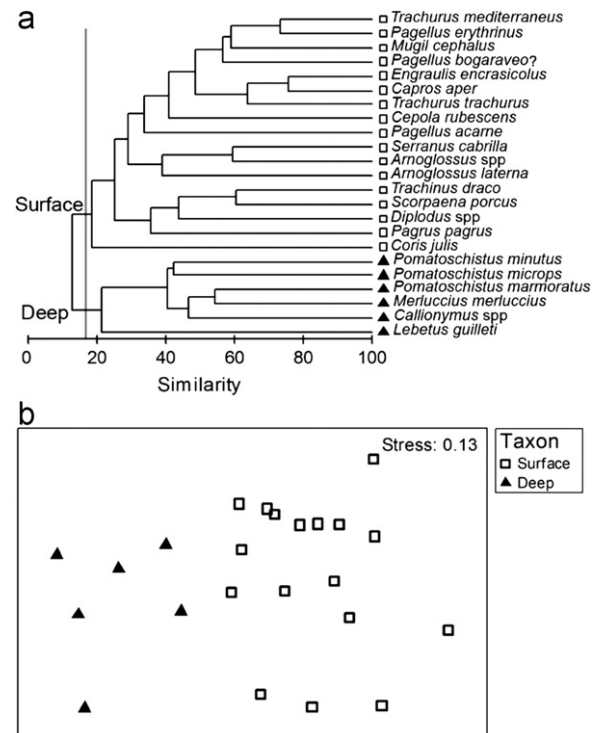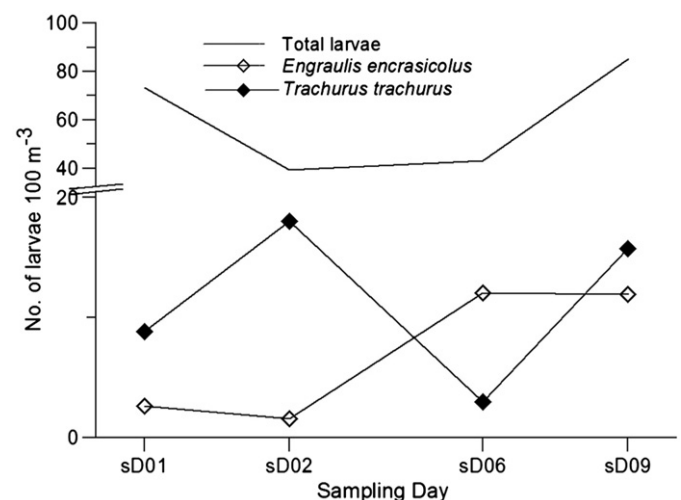 the summer larval fish assemblage in the region, during the daytime. Selection of daytime depths by fish larvae, based on temperature preferences, has already been suggested (Garrido et al., 2009; Haldorson et al., 1993). Nevertheless, the pattern of vertical distribution found in this study combined with observations that fish larvae disperse at night (Brewer and Kleppel, 1986; Gray, 1998; Heath et al., 1988; Leis, 1991) suggest that light intensity may also be an important factor in the vertical distribution of fish larvae in the region. The influence of light in the vertical distribution of fish larvae is supported by the results of a study carried out in the region, in July 2010 (Rodriguez et al., unpublished data). In general, vertical distributions were narrow and highly structured during the day-time and wider and mostly unstructured at night. All the above
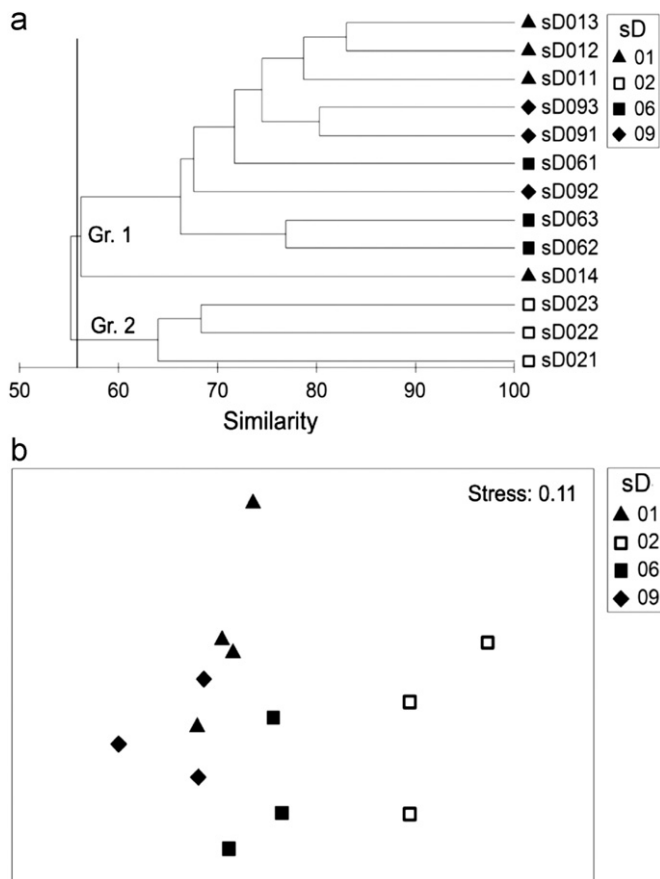
Fig. 9. (a) Sampling dendrogram resulting from the cluster analysis performed on a Bray–Curtis similarity matrix generated from the four root transformed larval fish concentrations at each replicate sampling day. The two identified clusters, separated at a 56% similarity threshold, are indicated. Sampling codes are the following: left two figures for sampling day and right figure for haul number. (b) two-dimensional MDS plot generated from the same similarity matrix as (a).

Table 4
Percentage contribution (contrib. %) and the cumulative percentage contribution (Cum. %) of taxa to the average similarity within each group, as determined by SIMPER analysis.

Taxon	Contrib. %	Cum. %
Group 1	Average similarity: 69.0	
Capros aper	11.7	11.7
Trachurus trachurus	11.3	23.1
Engraulis encrasicolus	11.1	34.2
Pomatoschistus marmoratus	7.7	41.9
Callionymus spp	6.6	48.5
Pagellus bogaraveo?	6.5	48.5
Trachurus mediterraneus	6.4	55.0
Mugil cephalus	6.3	67.6
Pagellus erythrinus	5.7	73.3
Arnoglossus spp	4.8	78.2
Trachinus draco	4.6	82.8
Pagellus acarne	3.6	86.4
Serranus cabrilla	3.5	89.9
Pomatoschistus minutus	2.8	92.8
Group 2	Average similarity: 68.0	
Trachurus trachurus	22.6	22.6
Capros apper	14.9	37.6
Pomatoschistus microps	13.4	51.0
Pomatoschistus minutus	10.6	61.6
Serranus cabrilla	10.0	71.6
Arnoglossus spp	10.0	81.5
Engraulis encrasicolus	4.1	85.6
Pomatoschistus marmoratus	4.0	89.6
Merlucius merlucius	3.8	93.4

supports findings that the vertical distribution of fish larvae is taxon-specific, independent of the physical stratification (Gray and Kingsford, 2003; Muhling and Beckley, 2007; Rodriguez et al., 2006; Röpke, 1993) and suggests that water temperature selection, light intensity and perhaps prey distribution are major factors in triggering this larval behavior. It is also important to highlight that fish larvae, in spite of their relatively small size, were able to maintain a defined pattern of vertical distribution during the daytime.

The different patterns of vertical distribution shown by larval fish taxa would determine their horizontal distribution and perhaps their fate in this region of coastal upwelling. As the coastal upwelling entails the offshore transport of surface waters, it also entails the shoreward transport of deeper waters. So, during upwelling, fish larvae with near-surface distribution will be transported offshore in the Ekman layer (John, 1985; John and Re, 1995; Rodriguez et al., 2006; Smith and Suthers, 1999). Since most larvae caught in this study have a shallow distribution, they would be susceptible to the offshore Ekman transport. The shallow distribution shown by most taxa contradicts the finding that taxa that reproduce during active upwelling show a broad vertical distribution, as an adaptive strategy to avoid the Ekman transport (Olivar, 1990). In contrast, the deep onshore flow would shoreward transport larvae with depth distribution (John, 1985; John and Re, 1995; Rodriguez et al., 2006; Smith and Suthers, 1999). In our case, the most important effect of this deep onshore transport would be either the maintenance of larvae of coastal-

shelf spawning species with deep distribution within the shelf, e.g. *Callionymus* spp, or the transport of larvae of shelf-break spawning species, e.g. *M. merluccius*, into the shelf, where the nursery areas for this species in the Bay of Biscay are located (Alvarez et al., 2004). Also, during events of westerly wind and the resulting eastward currents, larvae with surface distribution could undergo east-shoreward transport.

4.4. Temporal distributions

Sampling at a geographically fixed station, as in this study, implies sampling the different water masses with their load of plankton, including ichthyoplankton, which may pass through the location. The different larval fish assemblage found on sD02 would be the result of the hydrographic conditions recorded during 18 and 19 August. The westerly wind pulse and the associated south-eastward surface currents recorded on those days would move surface waters, together with their load of fish larvae, shoreward. These waters would be replaced by others coming from about the shelf-break, also with their load of fish larvae. Since comparatively very few neritic fish species spawn in that region, these waters would be poor in fish larvae. Precisely, the highest larval concentration was recorded on sD9, when summer upwelling conditions were almost fully recovered, and fish larvae would consequently be transported offshore in the Ekamn layer associated to coastal upwelling. The temporal pattern of larval concentration followed by *E. encrasicolus* larvae, a preferentially estuarine–coastal spawning species in the region (Arbault and Lacroix, 1977; Bellier et al., 2007; Re, 1996), agrees with the temporal evolution of the hydrography: low concentrations under westerly-shoreward transport and higher concentrations under upwelling-offshore transport. Also, the lower contribution of surface dwelling species to the cluster formed by samples collected on sD02 supports the idea that the different larval fish assemblage found on this sD was the result of the shoreward transport of surface waters

with their load of larvae. The undefined temporal pattern of concentrations followed by *T. trachurus* would be related with the spawning location of this species, from the coast to the shelf-break (Hureau, 1996). So, *T. trachurus* larvae would come from either the coastal or the outer shelf regions. In conclusion, short-term advective processes produced important short-term variability in the larval fish assemblage at the sampling location.

4.5. Conclusions

A strong westerly wind event at the beginning of the cruise Perplan 0808 altered the summer conditions of coastal upwelling in the Central Cantabrian Sea (Southern Bay of Biscay). The perturbation produced a response in the dynamics and in the hydrographic structure of the water column on the continental shelf. This hydrographic event did not affect the vertical distribution of fish larvae but accounted for significant temporal changes in larval fish assemblage structure and abundance. Results of this study also indicate that an Eulerian sampling, carried out at a single station, is not adequate to characterize the temporal distribution of the ichthyoplankton in this dynamic shelf region. Sampling at a single station implies sampling the water masses that pass through the location. This will give us a snapshot of the larval fish assemblage transported by the water mass that at the time of the sampling occupy the station. The scale of temporal changes would depend, among other factors, on the size of the larval patch and oceanographic processes, which influence movement and dispersion (Gray, 1996b). So, according to Gray, (1996b and references herein), the temporal monitoring of the larval fish assemblage in this hydrographically dynamic region requires multiple sampling sites embracing the whole distribution area of the larval fish assemblage.

Acknowledgments

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