



Vertical distribution and migration of fish larvae in the NW Iberian upwelling system during the winter mixing period: implications for cross-shelf distribution

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ABSTRACT

The vertical distribution and vertical migrations of fish larvae and implications for their cross-shelf distribution were investigated in the northern limit of the NE Atlantic upwelling region during the late winter mixing period of 2012. The average positive values of the upwelling index for February and March of this year were far from normal, although the average hydrographic conditions during the period of study were of downwelling and the water column was completely mixed. Fish larvae, most in the preflexion stage, were concentrated in the upper layers of the water column and their distribution was depth stratified, both day and night. However, the larval fish community was not structured in the vertical plane and fish larvae did not show significant diel vertical migration (DVM), although five species showed ontogenetic vertical migration. In regions of coastal upwelling and in the absence of DVM, the location of fish larvae in the water column is crucial for their cross-shelf distribution. Thus, the cross-shelf distribution of the six most abundant species collected in this study can be explained by the surface onshore flow associated with

coastal downwelling, retaining larvae of the coastal spawning species with a relatively shallow distribution in the shelf region and transporting larvae of slope spawning species onto the shelf. The wide vertical distribution shown by larvae of the offshore spawning species could be an adaptation of these species to ensure that some larvae reach the inshore nursery areas.

Key words: downwelling, fish larvae, ichthyoplankton, NW Iberian upwelling system vertical distribution, vertical migrations, winter mixing period

INTRODUCTION

The NW Iberian peninsula is considered the northern limit of the coastal upwelling that extends along the eastern boundary of the North Atlantic Ocean. At these latitudes in spring and summer, northerly winds favorable to coastal upwelling and an equatorward surface current over the shelf predominate (Wooster *et al.*, 1976; Haynes and Barton, 1990). In autumn and winter, southerly winds, favorable to coastal downwelling, prevail and the surface current reverses to poleward (Wooster *et al.*, 1976). Upwelling pulses are also frequent because the greater variability of atmospheric forcing occurs at scales shorter than seasonal (McClain *et al.*, 1986).

Fish larvae have heterogeneous vertical distributions (Heath, 1992). In general, they display species-specific vertical distributions (Ahlstrom, 1959; Leis, 1991; Röpke, 1993; Gray, 1996). Larvae of many fish species migrate vertically, on a diel basis (Ahlstrom, 1959; Röpke, 1989; Neilson and Perry, 1990; Auth *et al.*, 2007), or ontogenetically (Gorbunova *et al.*, 1986; Fortier and Harris, 1989; Paris and Cowen, 2004), with these migrations being species-specific (Fortier and Harris, 1989; Röpke, 1989, 1993). Fish larvae, like other zooplankton components, may follow two patterns of diel vertical migration (DVM): DVM type I and DVM type II (Neilson and Perry, 1990). Larvae that follow DVM type I move upwards at night while larvae that follow DVM type II move upwards

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during the daytime. DVM is often a size-related phenomenon, with the range of migration increasing with larval size (Neilson and Perry, 1990). It has also been reported that the beginning of DVM requires a minimum species-specific size (Landaeta and Castro, 2002, 2012), which in some cases has been related to the change from endogenous to exogenous feeding (Shojii *et al.*, 1999), or to behavioral changes associated with ontogeny, e.g., development of the caudal fin (Landaeta and Castro, 2002; Somarakis and Nikolioudakis, 2007). In thermally stratified waters, the presence and position of the thermocline has been considered a major factor in the vertical distribution and in the DVM of fish larvae, where the thermocline may represent either the upper or the lower boundary for their vertical distributions and DVMs (Ahlstrom, 1959; Coombs *et al.*, 1981; Southward and Barret, 1983; Smith and Suthers, 1999). Other studies, however, have found that vertical distributions and DVMs are not influenced by the presence of a thermocline but are related to larval behavior, associated with the vertical distribution of prey and/or predators (Fortier and Harris, 1989; Munk *et al.*, 1989; Olla and Davis, 1990; Röpke, 1993; Gray, 1996).

Vertical distributions of fish larvae are of central importance to their ecology because feeding, predation and larval transport vary considerably with depth (Huebert, 2008). In contrast, vertical migrations can be used to move between vertically stratified currents (Paris and Cowen, 2004) and their role is also recognized as a critical component of realistic models of larval fish dispersion (Hurst *et al.*, 2009). Therefore, knowledge of patterns of vertical distribution and vertical migration of fish larvae is key to understanding and predicting cross-shelf distributions in regions of coastal upwelling, such as our area of study, characterized by a two-layered circulation. The dynamics in these regions favours the offshore transport of surface meroplanktonic larvae in the Ekman layer, and the onshore transport of deeper living larvae by the onshore flow during upwelling events. During downwelling conditions the opposite occurs, the surface onshore flow favors the onshore transport of surface living larvae whereas deeper living larvae may be advected offshore (Farrell *et al.*, 1991; Smith and Suthers, 1999; Epifanio and Garvine, 2001; Queiroga and Blanton, 2005). Upwelling relaxation also favors larval retention and concentration in coastal waters (Farrell *et al.*, 1991; dos Santos *et al.*, 2008).

The maintenance of fish larvae in appropriate nursery areas, generally located inshore, or the transport to these areas are critical for fish populations, because year-class success and, consequently, recruitment sizes

are determined during the early life stages of fish (Hjort, 1914). In upwelling regions, fish larvae of inshore-shelf spawning species may follow different strategies to avoid offshore advection. They may migrate vertically between the two flow regimes, daily (Parrish *et al.*, 1981; Myers and Drinkwater, 1989; Landaeta and Castro, 2002) or ontogenetically (Gorbunova *et al.*, 1986), or spawning may take place during upwelling relaxation or adult fish may spawn demersal eggs (Parrish *et al.*, 1981). Fish larvae of offshore spawning species may use the onshore currents to reach the inshore nursery areas (Smith and Suthers, 1999; Landaeta and Castro, 2002, 2012).

Knowledge of the vertical distribution of fish larvae also has practical implications for sampling designs. According to Ahlstrom (1959), a prerequisite for any quantitative sampling program of pelagic fish eggs and larvae is the knowledge of their vertical distribution. Sampling to inappropriate depths can lead to under-sampling if the entire depth range of distribution of target species is not covered, or to waste of sampling time in the case of surface-dwelling species.

Despite the importance of the larval stage for fish populations, relatively little is known on the vertical distribution and migration of fish larvae off the Atlantic and Cantabrian coast of the Iberian Peninsula. Santos *et al.* (2006) studied the vertical distribution and the DVM of *Sardine pilchardus*. Studies dealing with the whole larval fish community are also scarce (John and Re, 1995; Garrido *et al.*, 2009; Rodriguez *et al.*, 2011), or were restricted to the very nearshore assemblages (Borges *et al.*, 2007) and none of them were conducted during the winter mixing period. In this paper, we study the vertical distribution, the vertical structure and DVM of the entire larval fish community and of selected taxa (those with ≥ 20 larvae caught, both day and night) off the NW Iberian Peninsula (NE Atlantic) during the winter mixing period. We also discuss implications that vertical distributions and migrations of fish larvae may have on their cross-shelf distribution.

MATERIAL AND METHODS

Sample collection and treatment

This study is based on zooplankton samples and hydrographic data collected during the Cramer 1203 cruise, carried out in the NW Iberian peninsula, NE Atlantic (Fig. 1), in later winter (from February 28 to March 13) 2012. A total of 76 stations, arranged in 15 transects perpendicular to the coastline, were sampled (Fig. 1). Transects were 8 miles apart, and the distance between stations was 4 miles. Stations were sampled at different times during both the day

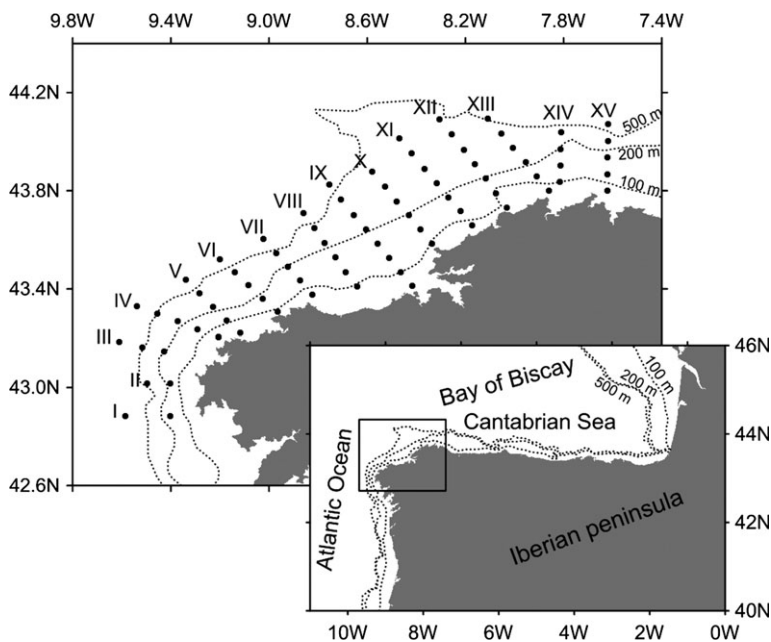


Figure 1. Location of the study area and sampling stations.

($N = 35$) and night ($N = 38$). Three stations were not included in the analysis because one of them was sampled at dawn (the zooplankton tow began at night but was completed after sunrise), and the other two because some samples were lost.

At every station, vertical profiles of conductivity, temperature and pressure were recorded with a SeaBird 25 CTD. Profiles were from the surface to 5 m above the bottom.

Local winds were measured by the 'Puertos del Estado' buoy, located at 43.50°N and 9.21°W. Upwelling index data were provided by Spanish Institute of Oceanography (available at <http://www.indicedeafloramiento.ieo.es>). Surface current maps were obtained from the regional oceanographic model system (ROMS) of the Spanish Institute of Oceanography.

Stratified zooplankton samples at five predefined and fixed depth strata (0–20, 20–40, 40–60, 60–100 and 100–200 m depth) were collected with a multiple opening/closing net MultiNet MiDi, 50 × 50 cm aperture (MultiNet Hydro-Bios Apparatebau), equipped with five nets of 200 μ m mesh size. The multinet, programmed to open/close at the predefined depths, was towed obliquely, sampling from 200 m depth (or ~10 m above the bottom at shallower stations) to the surface, at 2.5–3 knots and at a retrieval rate of 20 m per minute. Haul depth was monitored during every sampling by a Scanmar depth sensor mounted on the wire cable, 1 m above the net. The volume of water filtered in each stratum was measured by an electronic flowmeter located at the mouth of the

net. Samples were immediately preserved in a 5% solution of buffered formalin and seawater.

In the laboratory, mesozooplankton individuals were semi-automatically counted using an image analysis technique (Bachiller and Fernandes, 2011). A subsample of 5 mL from each sample was stained for 24 h with 0.1% eosin. The stained sample was scanned using the VUESCAN PROFESSIONAL EDITION 8.5.02 software Hamrick Software, Sunny Isles Beach, Florida, USA. www.hamrick.com, generating an image of 256 (eight-bit) colors and with a resolution of 2400 dpi. Images were processed using the Zoolmage (available at <http://sciviews.org/zoolmage/>) and the IMAGEJ 1.45s (available at <http://rsb.info.nih.gov/>) image analysis software. Each zooplankton individual was automatically counted, and its length measured. Mesozooplankton (size fraction 0.2–2 mm) counts were standardized to no. of individuals per m^3 .

All fish larvae were sorted from the samples and identified to the lowest taxonomic level possible. Selected taxa (those with ≥ 20 larvae caught, both day and night) were photographed and subsequently measured for standard length, using the IMAGEJ 1.45s software. Concentrations of fish larvae at each depth stratum were expressed as the number of individuals per 1000 m^3 . Abundances, number of larvae per 10 m^2 , were also calculated for each station.

Statistical analysis

The weighted mean depth (WMD) of mesozooplankton and fish larvae at each station was calculated as:

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

where n_i is the concentration of individuals at i th stratum and d_i is the mean depth of the i th stratum. WMDs were used to deal with the vertical distribution and DVM of mesozooplankton and fish larvae. The amplitude of DVM was calculated as the difference between the mean WMDs during day and night. A positive value indicates movement towards the surface during the night, or type I DVM, and a negative value indicates a downward movement during the night, or type II DVM (Neilson and Perry, 1990). Because DVM is often a size-related phenomenon, with larvae starting to migrate after yolk sac absorption (Neilson and Perry, 1990 and references herein), larvae of the most abundant species, *Micromesistius poutassou*, were divided into two size classes and their WMDs were also calculated. One of the size classes included larvae <4 mm and the other included larvae ≥ 4 mm. According to Russell (1976), the first size class would include yolk sac larvae and the second larvae with external feeding, and the transition between both larval phases would be around 3.0–3.3 mm. Differences in WMDs between day and night were assessed with Student's t -test for independent samples.

Diel (day/night)-depth differences in larval sizes for those taxa with enough larvae measured (at least 3 larvae per time -day and night- and strata) and the interactions between time and depth were analyzed using a two-factor ANOVA. For the other selected taxa, differences in larval size between day and night were assessed with Student's t -test for independent samples.

The relationship of the vertical distribution of fish larvae with the vertical distribution of mesozooplankton was examined using correlation analysis. We calculated Pearson's correlation coefficient of WMDs of total fish larvae and larvae of selected taxa with WMDs of mesozooplankton.

In t -test and two-factor ANOVA, data were tested for homogeneity of variance (Levene test) and $\log_{10}(x + 1)$ transformed if necessary. In both tests, the significance level was set at $P < 0.01$ to reduce the risk of a type I error (Underwood, 1997). When significant differences were found by two-factor ANOVA, Student–Newman–Keuls (SNK) tests were conducted to investigate significant groupings. Also, prior to the correlation analyzes, data were tested for normality (Kolmogorov–Smirnov test) and $\log_{10}(x + 1)$ transformed if necessary.

In the study of the vertical structure of the larval fish community, larval concentrations for each taxon per depth stratum with two or more taxa constituted a

sampling unit in the matrix used in the multivariate analysis. Differences in the larval fish community structure among the five depth strata within the time of the day (day/night) and between day and night were explored with the two-way analysis of similarities (ANOSIM), performed on a Bray–Curtis similarity matrix generated from the square root transformed data of larval fish concentrations. Data were transformed to down-weight the influence of more abundant taxa (Clarke, 1993). No further analyzes were carried out because the null hypothesis of no differences in the vertical structure of the larval fish could not be rejected (see Results).

Univariate analyzes were performed with SPSS v. 19.0. ANOSIM was performed with PRIMER 6.1.6 (Primer E Plymouth, UK. <http://www.primer-e.com/>).

RESULTS

Hydrography

During February and March 2012, the wind regime in our study area was quite anomalous for this time of the year with northerly winds, favorable to upwelling, blowing almost persistently (Fig. 2). This resulted in mean upwelling index values of $554 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ for February and $192 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ for March. These values are far from the historical (1967–2013) mean of $-692 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ for February and $-303 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ for March. However, during the time of the cruise, northerly winds pulses alternated with southerly wind pulses, favorable to downwelling (Fig. 2). This resulted in a mean upwelling index value of $-39.7 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ for the period of study. It must be pointed out that positive values of the upwelling index indicate coastal upwelling whereas negative values correspond to coastal downwelling.

For its part, the surface water layer (0–200 m depth) was completely mixed (Fig. 3).

Vertical and cross-shelf distributions

The mesozooplankton, mainly concentrated in the upper 60 m of the water column, showed a stratified distribution, both day and night (Fig. 4). At night, the greatest concentration was found at the 0–20 m depth stratum whereas during the day the greatest concentration was recorded at the 20–40 m depth stratum (Fig. 4). The average depth distribution for zooplankton, combining day and night samples, was of 40.5 m (SE; 10.7 m). The mean concentration of mesozooplankton organisms at each depth stratum by day and night is shown in Table 1.

The mean concentration of all fish larvae and that of selected taxa (22 in total) at each depth stratum by

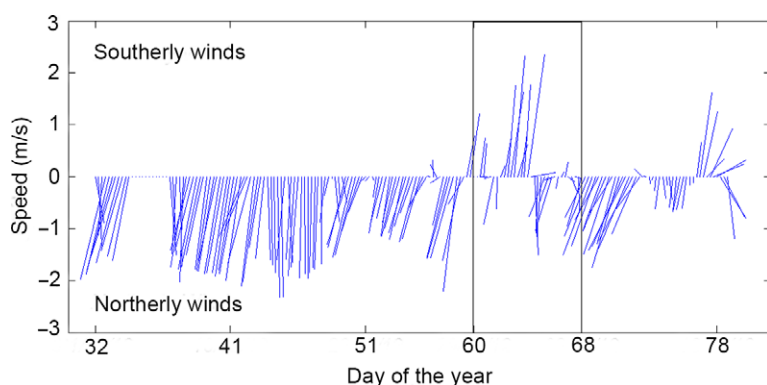
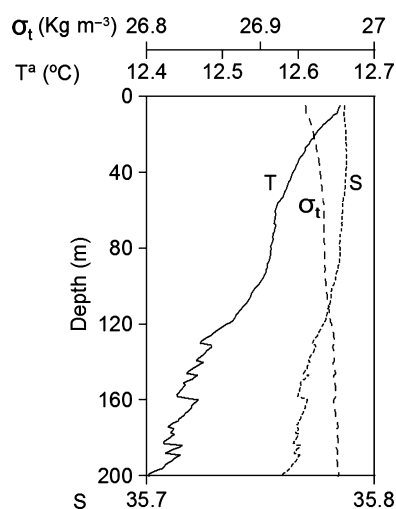


Figure 2. Wind direction and speed measured by the 'Puertos del Estado' buoy located at 43.50°N and 9.21°W. Vertical bars denote the beginning and the end of the cruise.

Figure 3. Average temperature (T), salinity (S) and density (σ_t) profiles.



day and night are also shown in Table 1. The average depth distribution of total fish larvae, combining day and night samples, was of 56.6 m (SE: 27.4 m). The larval fish community showed a similar pattern of vertical distribution to that of mesozooplankton (Fig. 4), with larvae likewise concentrated in the upper layers of the water column. Thus, 78.7% of the total larval fish concentration was found in the upper 60 m of the water column and 92.5% in the upper 100 m. The difference between both distributions was that the greatest concentration of fish larvae was found deeper, both during day and night (Fig. 4). In fact, the difference in the vertical distribution of both plankton components was significant (Student's *t*-test for paired samples, $P < 0.01$). In spite of this, there was a strong correlation between the vertical distributions of mesozooplankton and all fish larvae (Table 2).

Selected taxa also displayed stratified distributions that may be grouped into two major patterns. For the

first one, shown by most taxa, the bulk of larvae was concentrated in the upper 60 m of the water column, both during day and night. For some of these taxa, larvae were even absent from the 100–200 m depth stratum, during the day (*Arnoglossus laterna* and *Trisopterus minutus*) or at night (*Gaidropsarus vulgaris*, *Scomber scombrus* and *Spondyliosoma cantharus*) (Fig. 4 and Table 1). The second pattern was displayed by species whose larvae were relatively abundant at the 100–200 m depth stratum (*Argentina sphyraena*, *Lepidorhombus wiffiagonis*, *Maurolicus muelleri*, *Merluccius merluccius* and *M. poutassou*) (Fig. 4 and Table 1). In contrast, vertical distributions of the studied taxa were positively correlated with the vertical distribution of zooplankton, although these correlations were significant for four taxa only (Table 2). The average vertical distribution, day and night samples combined, for those four taxa was 51.0 m (SE: 37.1) for *Boops boops*, 67.4 m (SE: 33.8 m) for *M. merluccius*, 59.0 m (SE: 30.4 m) for *M. poutassou* and 40.7 m (SE: 28.9 m) for *Trisopterus luscus*. Of these four taxa, *M. merluccius* and *M. poutassou* showed a deeper distribution than zooplankton (Student's *t*-test for paired samples, $P < 0.01$).

Although the distribution of fish larvae was depth stratified, the two-way crossed ANOSIM ($r = 0.01$) shows that differences in community structure were neither significant between depths within time (day/night) nor among time.

As for cross-shelf distributions shown by the six most abundant taxa, larvae of *M. muelleri*, *M. merluccius* and *M. poutassou* were widespread over the study area, whereas larvae of *Sardina pilchardus*, *S. scombrus* and *T. minutus* were restricted to the shelf region (Fig. 5).

The length-frequency distribution of the six most abundant taxa is shown in Fig. 6. The number of fish larvae measured by day and night by taxon, the average of larval size by depth stratum and time (day/

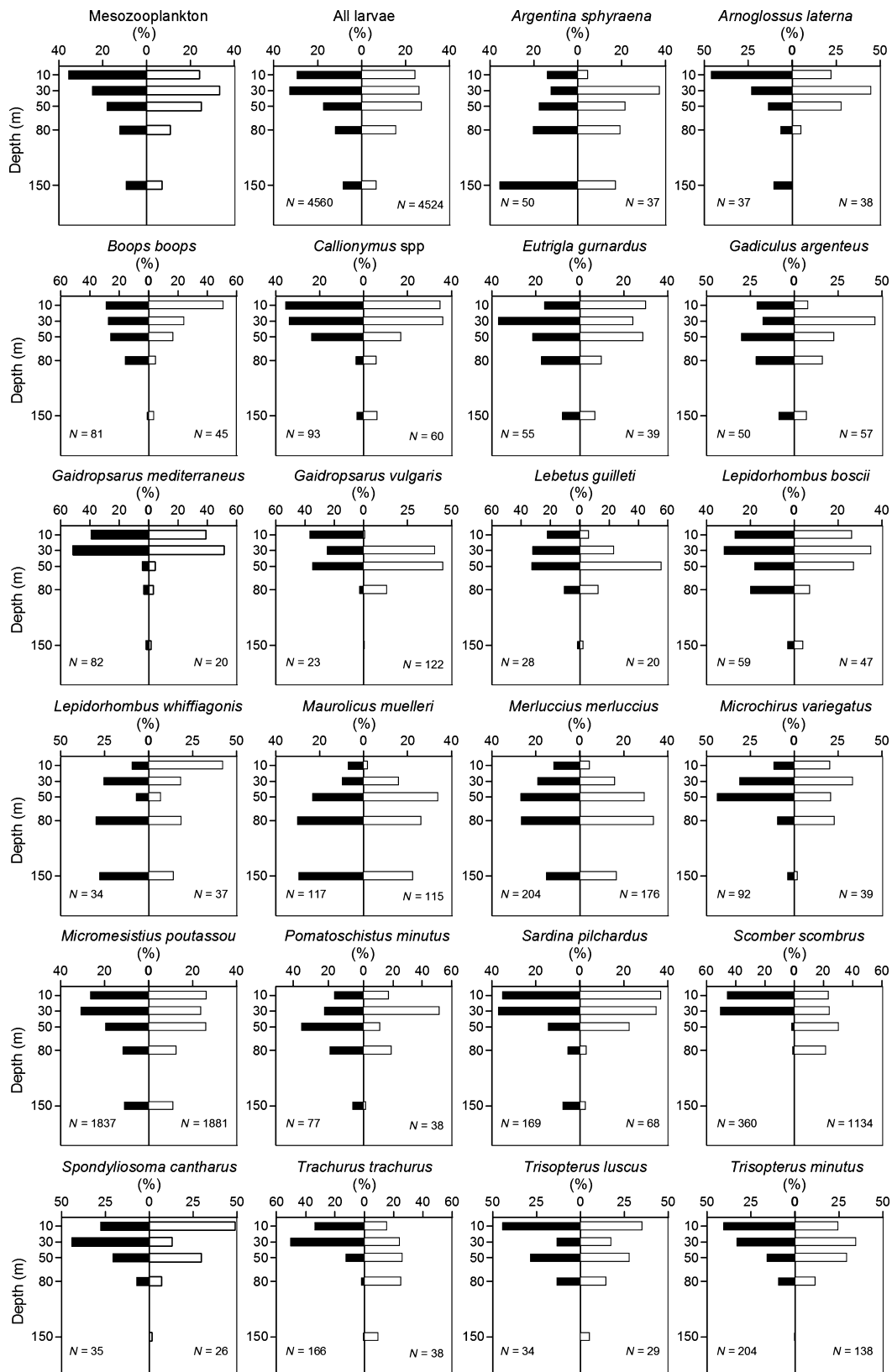
Figure 4. Mean vertical distribution of mesozooplankton and fish larvae during the day (open bars) and night (filled bars)

Table 1. The mean concentration and standard deviation of mesozooplankton (no. of individuals m^{-3}), all fish larvae and selected larval fish taxa (no. of larvae $1000\ m^{-3}$) per each depth stratum and time (Day, Night).

	0–20 m depth		20–40 m depth		40–60 m depth		60–100 m depth		100–200 m depth	
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
Mesozooplankton individuals	264 ± 262	313 ± 238	366 ± 879	217 ± 184	272 ± 451	159 ± 88	119 ± 85	107 ± 70	77 ± 71	83 ± 51
All fish larvae	973 ± 2561	1119 ± 1954	1044 ± 2600	1243 ± 2172	1088 ± 2860	657 ± 1176	619 ± 1762	453 ± 550	263 ± 547	318 ± 590
<i>Argentina sphyraena</i>	1 ± 8	5 ± 15	10 ± 25	4 ± 14	6 ± 29	6 ± 18	5 ± 12	7 ± 13	5 ± 15	13 ± 21
<i>Arnoglossus laterna</i>	8 ± 24	16 ± 45	16 ± 52	8 ± 22	10 ± 31	5 ± 15	2 ± 8	2 ± 6	–	4 ± 19
<i>Boops boops</i>	28 ± 124	18 ± 52	13 ± 72	17 ± 59	9 ± 40	16 ± 56	3 ± 9	10 ± 29	2 ± 7	1 ± 3
<i>Callionymus</i> spp	19 ± 53	21 ± 45	20 ± 42	20 ± 38	9 ± 39	14 ± 40	3 ± 11	2 ± 7	3 ± 11	2 ± 4
<i>Eutrigla gurnardus</i>	8 ± 20	8 ± 21	6 ± 17	17 ± 35	8 ± 19	10 ± 20	3 ± 8	8 ± 22	2 ± 7	4 ± 19
<i>Gadiculus argenteus</i>	4 ± 15	9 ± 27	23 ± 49	8 ± 19	11 ± 25	13 ± 35	8 ± 24	10 ± 20	4 ± 12	4 ± 10
<i>Gaidropsarus argenteus</i>	11 ± 25	20 ± 51	11 ± 30	27 ± 86	3 ± 12	2 ± 17	0 ± 2	2 ± 7	1 ± 4	1 ± 4
<i>Gaidropsarus mediterraneus</i>	1 ± 3	5 ± 14	29 ± 122	3 ± 12	32 ± 128	5 ± 15	9 ± 27	0 ± 2	0 ± 2	–
<i>Gaidropsarus vulgaris</i>	1 ± 8	5 ± 18	5 ± 16	8 ± 21	11 ± 28	8 ± 26	3 ± 8	3 ± 7	1 ± 3	0 ± 2
<i>Lebetus guilleti</i>	12 ± 27	12 ± 33	16 ± 32	14 ± 31	13 ± 47	8 ± 22	3 ± 9	9 ± 17	2 ± 6	1 ± 4
<i>Lepidorhombus boscii</i>	12 ± 49	3 ± 13	5 ± 20	8 ± 44	2 ± 8	2 ± 14	5 ± 16	9 ± 29	4 ± 12	9 ± 27
<i>Lepidorhombus whiffiagonis</i>	1 ± 6	6 ± 16	10 ± 30	8 ± 21	20 ± 31	19 ± 43	16 ± 25	25 ± 36	13 ± 16	24 ± 42
<i>Maurolicus muelleri</i>	5 ± 18	19 ± 38	19 ± 45	31 ± 62	34 ± 43	43 ± 83	39 ± 60	43 ± 71	19 ± 39	24 ± 28
<i>Merluccius merluccius</i>	5 ± 16	14 ± 29	12 ± 36	23 ± 51	17 ± 41	14 ± 36	4 ± 11	16 ± 32	2 ± 5	1 ± 4
<i>Microchirus variegatus</i>	398 ± 1284	401 ± 1023	360 ± 1167	467 ± 1147	395 ± 1269	299 ± 844	191 ± 490	178 ± 856	168 ± 503	170 ± 523
<i>Micromesistius poulassou</i>	6 ± 19	12 ± 33	18 ± 49	15 ± 31	4 ± 16	25 ± 55	7 ± 20	13 ± 26	0 ± 3	4 ± 15
<i>Pomatoschistus minutus</i>	29 ± 81	49 ± 110	27 ± 106	52 ± 138	18 ± 84	20 ± 53	2 ± 8	8 ± 17	2 ± 12	11 ± 51
<i>Sardina pilchardus</i>	268 ± 1335	110 ± 597	273 ± 1388	122 ± 534	355 ± 1935	5 ± 14	252 ± 1396	3 ± 7	2 ± 9	1 ± 3
<i>Scomber scombrus</i>	14 ± 46	7 ± 23	4 ± 16	11 ± 56	9 ± 27	5 ± 30	2 ± 12	2 ± 7	0 ± 3	–
<i>Spondylosoma cantharus</i>	5 ± 24	38 ± 193	7 ± 22	57 ± 276	8 ± 29	15 ± 75	8 ± 23	2 ± 6	3 ± 11	1 ± 4
<i>Trachurus trachurus</i>	10 ± 28	17 ± 40	5 ± 19	5 ± 20	8 ± 27	11 ± 32	4 ± 14	5 ± 16	2 ± 7	–
<i>Trisopterus luscus</i>	32 ± 113	63 ± 136	45 ± 114	51 ± 116	39 ± 87	25 ± 48	15 ± 36	15 ± 35	–	1 ± 4
<i>Trisopterus minutus</i>										

Table 2. Pearson's correlation coefficients between the vertical distribution [weighted mean depth (WMDs)] of fish larvae and mesozooplankton.

Mesozooplankton	
<i>Argentina sphyraena</i>	0.52
<i>Arnoglossus laterna</i>	0.27
<i>Boops boops</i>	0.68*
<i>Callionymus</i> spp	0.27
<i>Eutrigla gurnardus</i>	0.33
<i>Gadiculus argenteus argenteus</i>	0.43
<i>Gaidropsarus mediterraneus</i>	0.26
<i>Gaidropsarus vulgaris</i>	0.33
<i>Lebetus guilleli</i>	0.46
<i>Lepidorhombus boscii</i>	0.34
<i>Lepidorhombus whiffiagonis</i>	0.29
<i>Maurolicus muelleri</i>	0.35
<i>Merluccius merluccius</i>	0.41*
<i>Microchirus variegatus</i>	0.47
<i>Micromesistius poutassou</i>	0.50*
<i>Pomatoschistus minutus</i>	0.45
<i>Sardina pilchardus</i>	0.15
<i>Scomber scombrus</i>	0.37
<i>Spondyliosoma cantharus</i>	0.40
<i>Trachurus trachurus</i>	0.53
<i>Trisopterus luscus</i>	0.69*
<i>Trisopterus minutus</i>	0.21
All larvae	0.63*

* $P < 0.01$.

night) and results of the two-factor ANOVA (or alternatively t -test), performed on larval sizes, are presented in Table 3. These results show that sufficient larvae to perform the two-factor ANOVA were measured for 9 out of 22 selected taxa. Of these, sufficient larvae were measured at the five depth strata only for *M. merluccius* and *M. poutassou*. For the other seven taxa, differences in larval sizes were assessed for the four upper sampling strata. Differences in day/night larval sizes were significant for six taxa (Table 3). For four of them, *G. vulgaris*, *M. muelleri*, *M. poutassou* and *T. minutus*, larvae caught at night were significantly larger than larvae caught during the daytime (Table 3). Nevertheless, for *Microchirus variegatus* and *Trachurus trachurus*, larvae caught during the daytime were significantly larger (Table 3). Differences in larval size with depth were significant for five taxa. The main feature of the vertical distribution of larval sizes was that, apart from *S. scombrus*, the smaller larvae were caught at the 100–200 m depth stratum. In the case of *S. scombrus*, the smallest larvae were caught at the 20–40 m depth stratum (Table 3). The interaction between time and depth was not significant for any of the nine taxa studied (Table 3). As for

differences in WMDs between day and night for the two larval size classes of *M. poutassou* (<4 mm, mean size of 2.7 mm, SD: 0.5; ≥ 4 mm, mean size of 5.3 mm, SD: 0.9) were not significant (Student's t -test, $P > 0.01$ in both cases).

Vertical migrations

Mesozooplankton and most larval fish taxa showed DVM type I. The larval fish community and eight taxa performed DVM type II. *Sardine pilchardus* did not perform any diel movement (Table 4). The range of vertical displacement was relatively small and differences in WMDs between day and night were not statistically significant for mesozooplankton, the larval fish community or any single larval fish taxon (Student's t -test, $P > 0.01$ in all cases).

DISCUSSION

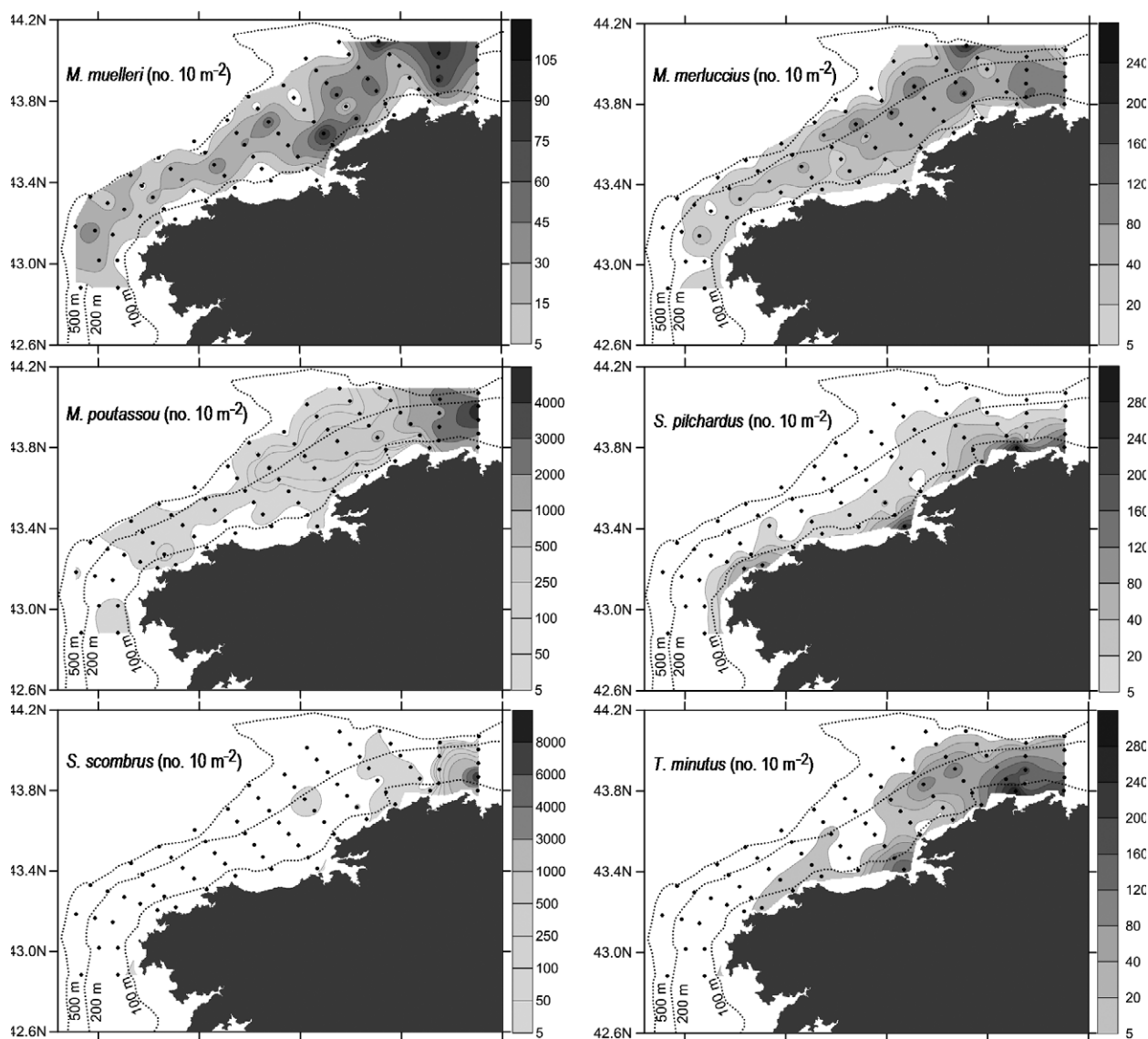
Hydrography

This study was carried out in the late winter, when the upper water column was well mixed, a typical situation for the time of the year (Castro *et al.*, 2006), and when downwelling conditions are expected. However, during the cruise, northerly winds, favorable to upwelling, alternated with southerly winds, favorable to downwelling and the average upwelling index value for the period of the study indicated weak downwelling. Accordingly, currents over the shelf were either poleward or undefined (Rodriguez, unpublished data). The prevalence of coastal downwelling conditions during the study period was supported by the cross-shelf distribution of the six most abundant species. Thus, larvae of species with coastal-shelf spawning (e.g., *S. pilchardus*, *S. scombrus* and *T. minutus*) and whose larvae have a relatively shallow distribution, as shown below, were restricted to the shelf region, presumably by the onshore Ekman flow associated with coastal downwelling. Larvae of species that reproduce over the slope (e.g., *M. muelleri*, *M. merluccius* and *M. poutassou*) were spread over the whole shelf, presumably by the surface onshore Ekman transport associated with coastal downwelling. The onshore transport of *M. muelleri*, *M. merluccius* and *M. poutassou* larvae is supported by the offshore–onshore increase in larval size shown by these three species (Fig. 7).

Vertical distributions

The concentration of most fish larvae in the upper 100 m of the water column agrees with previous findings in stratified (Gray, 1996; Conway *et al.*, 1997; Auth *et al.*, 2007) and non-stratified waters (Gray, 1996; Conway *et al.*, 1997; Sabates, 2004). Also, the

Figure 5. Horizontal distribution of fish larvae of the six most abundant species.



stratified distribution shown by fish larvae, both during day and night, has already been reported in thermally stratified (Ahlstrom, 1959; Southward and Barret, 1983; Coombs *et al.*, 2001; Olivar *et al.*, 2010) and non-stratified waters (Fortier and Harris, 1989; Röpke, 1989; Sabates, 2004; Olivar *et al.*, 2010).

The vertical distribution of fish larvae has often been related to the thermal stratification of the water column that would help them to maintain their depth distribution. The thermocline may also function as an upper or lower barrier for their distribution (Ahlstrom, 1959; Boehlert *et al.*, 1985; Moser and Pommeranz, 1999; Smith and Suthers, 1999). Therefore, in the homogenous environment of our area of study, fish

larvae had to actively swim to maintain their vertical position in the water column, because larvae are generally denser than water (Heath, 1992). According to Leis (2006), the vertical distribution of fish larvae is under strong behavioral control from the time of hatching. The ability of fish larvae (yolk-sack included, without developed swimbladder) to control their position in the water column, even in well-mixed environments, is well documented (e.g., Fortier and Harris, 1989; Leis, 2007; Hurst *et al.*, 2009; Kunze *et al.*, 2013). This enables larvae to select favorable conditions or to avoid unfavorable ones (Olla and Davis, 1990; Röpke, 1993). In the absence of thermal stratification, other factors than a thermocline have to

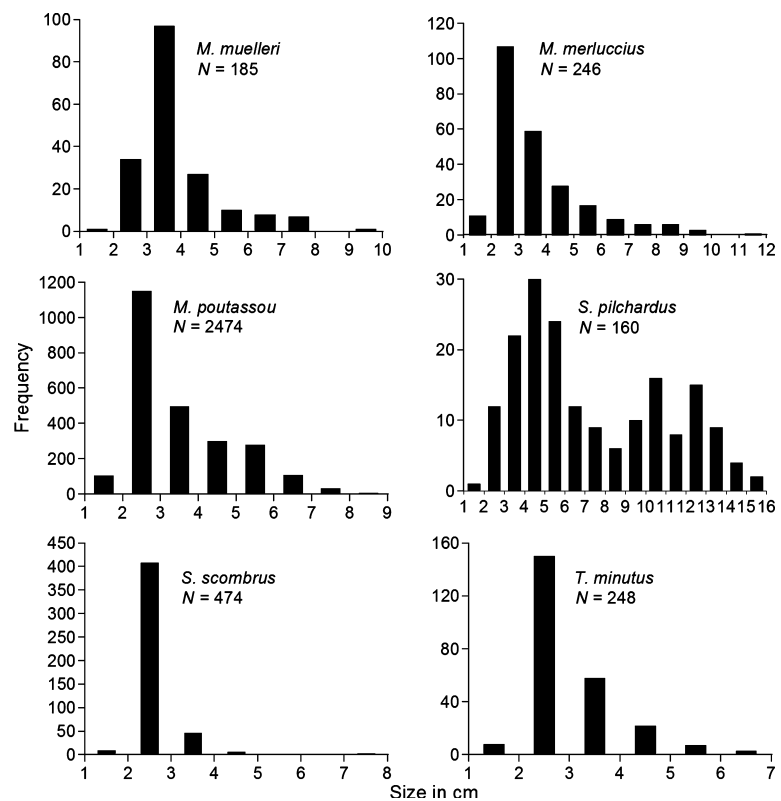


Figure 6. Length-frequency distribution of the six most abundant species.

be involved in the vertical distribution of fish larvae. In this way, several authors have suggested that the vertical distribution of fish larvae is determined by feeding conditions in the water column (e.g., Fortier and Harris, 1989; Munk *et al.*, 1989; Röpke, 1993).

The relatively strong correlation found between the vertical distribution of fish larvae and mesozooplankton indicates some relationship between them. This relationship was also supported by the relatively high and significant correlation ($r = 0.55$, $P < 0.01$) found between the horizontal distribution of larval fish abundance with mesozooplankton biomass (Rodríguez, unpublished data). This relationship between these two zooplankton components could be trophic, with fish larvae preying on or being preyed upon by mesozooplankton (Bailey, 1984; Hunter, 1984). However, before discussing this relationship, two aspects must be taken into consideration. That is, the small size of the larvae collected in this study and the vertical segregation of fish larvae and mesozooplankton. As for the small size of the fish larvae collected, most of the taxa showed mean sizes around those reported for their yolk sack stages by Russell (1976), so most of the exogenous feeding larvae should be first feeding larvae that mainly rely on microzooplankton (Hillgruber and Kloppmann, 2001). An exception to the general rule

that the size of food ingested increases with larval size (Hunter, 1984) is *M. merluccius*, which does not exhibit ontogenetic changes in the type or size of prey (Morote *et al.*, 2011). Therefore, considering that mesozooplankton also feed on microzooplankton and even on fish larvae (Hunter, 1984; Fortier and Harris, 1989; Kleppel, 1993), the vertical segregation of fish larvae and mesozooplankton could be either to avoid competition for prey with mesozooplankton, in that larval prey can be significantly reduced by zooplankton feeding (Fortier and Harris, 1989), or because larval fish concentration in the layer of the highest mesozooplankton concentration has been reduced by zooplankton predation. Another possibility is that fish larvae avoid the layer of maximum concentration of mesozooplankton to prevent being preyed upon by zooplankton (Fortier and Harris, 1989). However, as we do not have data either on the vertical distribution of microzooplankton or on zooplankton predation on fish larvae, we can only speculate on these issues. Nevertheless, the small size of the fish larvae caught, which makes them suitable prey for a wide range of carnivorous zooplankton, along with the deeper distribution shown by *M. merluccius* larvae (which do not compete for food with mesozooplankton) in relationship to mesozooplankton would support the idea that larval fish

Table 3. No. of fish larvae of selected taxa measured by day and night, mean larval size per depth stratum and time (Day/Night), results of the two-factor ANOVA testing for differences in larval size between time (Day/Night) and depth and results of the SNK test (significant differences are indicated by different superscript letters). Results of the t-test used with taxa for which there were no enough larvae to be submitted to the two-factor ANOVA are also included. (NA: data not available; NS: not significant).

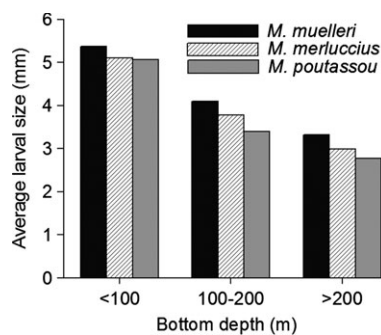
	No. of larvae measured		Mean larval size per depth stratum												Two-factor ANOVA <i>P</i> -values					
			0–20 m				20–40 m				40–60 m							60–100 m		
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Time: Day/Night	Depth	Time × depth	
<i>Argentina sphyraena</i>	30	45	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	—	—	—
<i>Arnoglossus laterna</i>	21	21	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	—	—	—
<i>Boops boops</i>	41	58	2.3	2.7	2.3	2.5	2.4	2.5	2.4	2.5	2.4	2.5	2.6	2.4	2.6	2.4	2.4	NS	NS	NS
<i>Callionymus</i> spp	47	75	1.9	1.9	2.0	2.0	2.1	1.7	2.1	1.7	2.1	1.7	1.9	2.4	1.9	2.4	2.4	NS	NS	NS
<i>Eurigla gurnardus</i>	21	50	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	—	—	—
<i>Gadiculus argenteus argenteus</i>	46	29	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	—	—	—
<i>Gaidropsarus mediterraneus</i>	19	77	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	—	—	—
<i>Gaidropsarus vulgaris</i> *	87	20	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	—	—	—
<i>Lebetus guilleti</i>	20	28	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	—	—	—
<i>Lepidorhombus boscii</i>	36	46	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	—	—	—
<i>Lepidorhombus whiffiagonis</i>	13	10	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	—	—	—
<i>Maurolicus muelleri</i> *	91	94	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	—	—	—
<i>Merluccius merluccius</i>	117	129	6.9	4.5	3.2	4.2	3.3	4.4	3.3	4.4	3.3	4.4	3.7	3.7	3.7	3.0	3.2	NS	<0.01	NS
<i>Microchirus variegatus</i>	27	76	3.8	2.8	3.4	3.1	3.0	2.3	3.0	2.3	3.0	2.3	3.0	2.2	3.0	2.2	NA	NA	<0.01	NS
<i>Micromesistius poulassou</i>	1251	1223	2.6	3.5	3.4	4.4	3.3	4.1	3.3	4.1	3.3	4.1	3.2	3.7	3.2	3.7	3.1	3.5	<0.01	NS
<i>Pomatoschistus minutus</i>	29	66	3.4	4.3	3.4	4.2	2.7	4.1	2.7	4.1	2.7	4.1	3.7	4.3	3.7	4.3	NA	NA	NS	NS
<i>Sardina pilchardus</i>	49	131	7.0	7.4	5.3	7.4	5.4	9.6	5.4	9.6	5.4	9.6	10.2	10.3	10.2	10.3	NA	NA	NS	NS
<i>Scomber scombrus</i>	356	118	2.8	2.6	2.7	2.4	2.8	2.9	2.7	2.4	2.8	2.9	2.7	3.0	2.7	3.0	NA	NA	NS	<0.01
<i>Spondyliosoma cantharus</i>	14	3	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	—	—	—
<i>Trachurus trachurus</i> *	30	107	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	—	—	—
<i>Trisopterus luscus</i>	17	26	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	—	—	—
<i>Trisopterus minutus</i>	80	168	2.7	2.9	2.9	3.2	2.9	3.6	2.9	3.6	2.9	3.6	2.7	2.6	2.7	2.6	NA	NA	<0.01	NS
SNK test (<i>P</i> < 0.01)																				
<i>Merluccius merluccius</i>																				
<i>Microchirus variegatus</i>																				
<i>Micromesistius poulassou</i>																				
<i>Scomber scombrus</i>																				
<i>Trisopterus minutus</i>																				
0–20 m ^a > 20–40 m ^{ab} > 40–60 m ^{ab} > 60–100 m ^{ab} > 100–200 m ^{bc}																				
20–40 m ^a > 0–20 m ^{ab} > 40–60 m ^{bc} > 60–100 m ^{cd}																				
60–100 m ^a > 20–40 m ^a > 40–60 m ^a > 0–20 m ^a > 100–200 m ^b																				
40–60 m ^a > 60–100 m ^a > 0–20 m ^a > 20–40 m ^b																				
20–40 m ^a > 40–60 m ^a > 0–20 m ^{ab} > 60–100 m ^{a,b}																				

*T-test significant at $P < 0.01$.

Table 4. Daytime weighted mean depth (DWMD) and amplitude of diel vertical migration (DVM, m) of mesozooplankton, all fish larvae and individual larval fish species. Negative values indicate reverse vertical migration (deeper at night than during the day).

	DWMD	DVM
Mesozooplankton	41.9	2.7
All fish larvae	54.6	-3.8
<i>Argentina sphyraena</i>	69.0	-7.5
<i>Arnoglossus laterna</i>	29.3	-0.5
<i>Boops boops</i>	53.4	3.9
<i>Callionymus spp</i>	31.7	-13.2
<i>Eutrigla gurnardus</i>	54.4	19.9
<i>Gadiculus argenteus argenteus</i>	44.9	-20.8
<i>Gaidropsarus mediterraneus</i>	45.3	6.3
<i>Gaidropsarus vulgaris</i>	43.5	19.3
<i>Lebetus guilleti</i>	58.9	23.1
<i>Lepidorhombus boscii</i>	43.6	-8.3
<i>Lepidorhombus whiffiagonis</i>	52.8	0.2
<i>Maurolicus muelleri</i>	85.1	8.3
<i>Merluccius merluccius</i>	70.2	5.0
<i>Microchirus variegatus</i>	48.4	8.7
<i>Micromesistius poutassou</i>	56.5	-4.8
<i>Pomatoschistus minutus</i>	36.0	-5.1
<i>Sardina pilchardus</i>	34.0	0.0
<i>Scomber scombrus</i>	31.6	-6.9
<i>Spondylusoma cantharus</i>	46.6	11.5
<i>Trachurus trachurus</i>	50.2	4.0
<i>Trisopterus luscus</i>	48.2	15.0
<i>Trisopterus minutus</i>	44.7	11.3

Figure 7. Onshore-offshore distribution of *Maurolicus muelleri*, *Merluccius merluccius* and *Micromesistius poutassou* average larval sizes grouped by bottom depth strata, as follows: <100, 100–200 and >200 m depth.



concentration in the layer of maximum mesozooplankton concentration had been reduced by zooplankton predation.

The two patterns of vertical distribution shown by larval fish taxa seem to be related to adult distributions

and their spawning site in the water column. The first pattern was shown by larvae of epipelagic (e.g., *S. pilchardus* and *S. scombrus*), benthopelagic (e.g., *T. luscus*) or demersal (e.g., *T. minutus*) fish species with a relatively shallow distribution (Whitehead *et al.*, 1984–1986; Froese and Pauly, 2013). According to these authors, these species either spawn in the surface layer, in the coastal region (e.g., *S. pilchardus*) or over the shelf (e.g., *S. scombrus*) or on the bottom in relatively shallow waters (e.g., *T. luscus* and *T. minutus*). The second pattern, shown by taxa with larvae relatively abundant at the 100–200 m depth stratum, corresponds with demersal (e.g., *Argentina sphyraena*), mesopelagic (e.g., *M. muelleri* and *M. poutassou*) or benthopelagic (e.g., *M. merluccius*) fish species, with a relatively deep distribution (Whitehead *et al.*, 1984–1986; Froese and Pauly, 2013). We do not have information on the spawning location in the water column for *A. sphyraena*. Nonetheless, *M. muelleri* spawns over the slope with the maximum spawning located between 100 and 400 m depth (John and Kloppmann, 1989). *Micromesistius poutassou* also spawns over the slope at depths of about 250–500 m (Coombs *et al.*, 1981). In the Bay of Biscay, *M. merluccius* spawns close to the 200 m isobath (Alvarez *et al.*, 2004) and, according to Coombs and Mitchell (1982), this species would spawn over the upper 150 m of the water column.

Although it is difficult to compare with other regions because of differences in the sampling resolution and sampling depths, for those species collected in this study and for which we have information on their vertical distribution in NE Atlantic and/or the Western Mediterranean regions, either during the mixing period (*A. laterna*, *Boops boops*, *Gadiculus argenteus*, *M. muelleri*, *M. merluccius*, *M. variegatus*, *M. poutassou*, *S. scombrus*, *S. pilchardus*, *T. trachurus*, *T. luscus* and *T. Minutus*) or/and the summer stratified period (*A. laterna*, *M. muelleri*, *M. merluccius*, *S. pilchardus* and *T. trachurus*), they showed relatively similar vertical distributions in both regions and under both environmental conditions (Coombs *et al.*, 1981; John, 1985; John and Kloppmann, 1989; Röpke, 1989; Olivar and Sabates, 1997; Sabates, 2004; Rodriguez *et al.*, 2006, 2011; Olivar *et al.*, 2010; Moyano *et al.*, 2014). This suggests that the vertical distribution ranges of fish larvae are species specific and independent of the local environmental conditions (Ahlstrom, 1959; Röpke, 1993; Sabates, 2004). However, the spawning location in the water column could determine the lower limit of distribution ranges.

For its part in regions of coastal upwelling/downwelling the wide vertical distribution shown by the early life stages of fish species that spawn offshore

would be an advantage, because during upwelling, the deep living larvae could be transported to the inshore nursery areas by the deep onshore Ekman flow while during downwelling the surface living larvae would be subject to the surface onshore Ekman transport. So, this wide distribution could be a strategy of the off-shore spawning species to ensure that at least a part of their offspring reaches the appropriate nursery areas over the shelf. The presence of *M. muelleri*, *M. Merluccius* and *M. poutassou* larvae over the whole study area and the shoreward increase in their sizes indicate an onshore transport of these larvae.

The absence of differences in the larval fish community structure in the vertical plane indicates that the upper water column was inhabited by the same larval fish assemblage, both day and night. This could be related to both the absence of DVM and with the absence of a thermocline that would allow the mixture of larval fish species which, in the presence of a thermocline, would display different vertical distributions (e.g., Ahlstrom, 1959; Southward and Barret, 1983; Röpke, 1993). This also indicates that sampling to a 100 m depth is sufficient to characterize the larval fish community of the region during the autumn–winter mixing period and, given the concentration of the large majority of fish larvae in the upper 100 m, to have an accurate approximation of the true larval fish abundance of the region.

The larger-sized larvae collected at night suggest net avoidance by these larvae during the daytime. Nonetheless, the absence of significant differences between day and night in larval fish abundance goes against net avoidance (Smith and Richardson, 1977). A possible explanation for the absence of differences in larval fish abundances between day and night is that larval fish predators (including planktivorous fish) were concentrated at depth during the day, migrating upwards at night to feed, reducing in this way the number of smaller larvae that are most susceptible to predation (Fortier and Harris, 1989). In contrast, the higher catchability of larger larvae at night could compensate for the reduction in number of the smaller larvae, accounting for the absence of significant day/night differences in larval fish abundances.

It is difficult to explain why larvae of *M. variegatus* and *T. trachurus* caught during the day were larger than those caught at night. If these species have a coastal spawning, larvae caught offshore should be larger. In this way, the difference in day/night larval sizes could be explained by the fact that most of the off-shore stations, where larger larvae should be found, were sampled mostly during the day.

Vertical migrations

The difficulties involved in the study of DVM of fish larvae are significant (see Pearre, 1979), especially considering the main limitations of our sampling strategy, which was not specifically designed to study DVM. We have compared samples collected at different times of day and night and different locations (shelf and shelf break), although with quite similar environmental conditions. The thickness of the strata, mainly the 60–100 and 100–200 m depth stratum, could exceed the migration range of some individuals. The smallest average vertical migration that we could detect is around 20 m; thus, DVM less than that would not be detected. Although a diel displacement of 30 m is not exceptional for larger larvae, it may be excessive for newly hatched larvae (Brodeur and Rugen, 1994). Our sampling depth did not cover the entire distribution range of some of the larval fish taxa studied. This is the case of *M. muelleri* (John and Kloppmann, 1989), *M. poutassou* (Coombs *et al.*, 1981) and *M. merluccius* (Coombs and Mitchell, 1982; Olivar *et al.*, 2003) and probably other species. The accuracy of the amplitude estimation is related to the abundance of organisms. Thus, apart from the mesozooplankton, the larval fish community and the species *M. poutassou* and perhaps *M. muelleri*, *M. merluccius* and *S. scombrus*, the other taxa studied were in relatively low abundance. Another factor that would limit the accuracy of our DVM estimates is the small size of the larvae collected. According to the larval fish size distribution (Fig. 6) and the mean larval size of selected taxa (Table 2) practically all fish larvae were in the preflexion stage (Russell, 1976). Despite these limitations, given the paucity of previous studies on the subject in the region and the relative paucity of studies on DVM of fish larvae in general, such an investigation is fully justified.

In our study, the absence of significant differences in WMDs between day and night and the relatively small range of daily displacement shown by mesozooplankton, the larval fish community and by most of the taxa studied suggest little or no DVM. DVM in fish larvae is often a facultative process and vertical migration patterns can be modified by environmental conditions, mainly temperature but also by food availability, in the local environment (Fortier and Leggett, 1983; Munk *et al.*, 1989; Neilson and Perry, 1990). Whether the vertical distribution of fish larvae was conditioned by the vertical distribution of their food, as mentioned above, and zooplankton seemed not to perform DVM, it would be an appropriate strategy for fish larvae not to migrate in order to remain close to their food

resources. However the absence of DVM may also have a negative consequence by not allowing larvae to take advantage of the two-layered circulation characteristic of upwelling/downwelling regions (Miller and Morgan, 2013). The interaction of DVM with the physics of the ocean to control larval dispersal has already been documented for meroplanktonic larvae of invertebrate neritic species (e.g., dos Santos *et al.*, 2008) and also for fish larvae (Parrish *et al.*, 1981; Myers and Drinkwater, 1989; Auth *et al.*, 2007).

Although DVM is often a facultative process, in some larval fish species this is also a size-related phenomenon (Neilson and Perry, 1990), with larvae beginning to migrate when they reach a minimum size (Fortier and Leggett, 1983; Landaeta and Castro, 2002, 2012). Therefore, the relatively small-sized larvae caught in this study could account for the absence of DVM. This would be the case for e.g., *S. pilchardus*, one of the few species collected in this study for which its size-related DVM is relatively well documented in the NE Atlantic (Rodríguez *et al.*, 2006; Santos *et al.*, 2006; Garrido *et al.*, 2009) and in the Mediterranean Sea (Olivar *et al.*, 2001). Larger sardine larvae, like other clupeids, move to the surface at night to swallow air to fill their swimbladder, in order to save the energy required to maintain their position in the water column during the resting period (Hunter and Sanchez, 1976; Santos *et al.*, 2006). The diel rhythm of swimbladder inflation/deflation is initiated at a size of around 12.5 mm (Re, 1986). Therefore, *S. pilchardus* larvae (average 6.3 and 7.4 mm for larvae collected during the day and at night, respectively) were quite below the threshold size to perform DVM. Other species caught in this study that would be in the same situation as *S. pilchardus* were *S. scombrus* and *M. merluccius*. Shojii *et al.* (1999) reported that DVM in *S. scombrus* larvae begins after yolk sac absorption. The size of *S. scombrus* larvae caught in this study (average 2.7 for larvae collected during the day and 2.5 mm for larvae collected at night) were also quite below the minimum size, 4.5 mm, of the larvae with the yolk sack fully absorbed (Russell, 1976). We do not have information on DVM in *M. merluccius*. However, a *Merluccius* species, *M. gayi*, has been reported to start DVM at the size of 7.0 mm (Landaeta and Castro, 2012), significantly larger than the *M. merluccius* larvae caught in this study (average 3.4 and 3.9 mm for larvae collected during the day and at night, respectively). In contrast, the non-significant differences between day and night for WMDs of the two size classes of *M. poutassou* suggest that, at least in this species, DVM was not a size-dependent phenomenon.

Although there is no evidence for significant DVM, the difference in larval size between strata for *M. merluccius*, *M. poutassou*, *M. variegatus*, *S. scombrus* and *T. minutus* suggest Ontogenetic Vertical Migration (OVM). Data in Table 4 suggest an upward OVM for these species, except for *S. Scombrus*. OVM has been proposed as a process to maximize the encounter rate of fish larvae with their food (Lafontaine and Gascon, 1989; Dickmann *et al.*, 2007), to avoid predation (Fortier and Harris, 1989) and for larval retention in or transport to suitable nursery grounds (Gorbunova *et al.*, 1986; Paris and Cowen, 2004). Given that mesozooplankton, and probably microzooplankton, are concentrated in surface layers, this upward OVM would match the vertical distribution of larger larvae of these species with the vertical distribution of their food and place these larvae in the Ekman layer, of around 45 m thick in winter, in the region (Cabanas, 1999).

With respect to the patterns of OVM followed by these five species, previous studies (Coombs and Mitchell, 1982) found no OVM in *M. merluccius*, while, *M. poutassou* showed the same pattern of OVM as reported for this species by Coombs *et al.* (1981). For its part, *M. variegatus* followed an opposite pattern of OVM to that found for this species by Fortier and Harris (1989). The pattern of OVM shown by *S. scombrus* did not agree either with the OVM reported for this species by Ware and Lambert (1985). These authors found larger larvae distributed in the surface layers. Coombs *et al.* (1981) also reported for this species an OVM from deeper layers. We do not have information on the OVM in *T. minutus*. In summary, in some cases there is an agreement with previous studies and in others not. The small size of the larvae caught in this study should be taken into consideration insofar as OVM, as the name indicates, is also a size-related phenomenon.

It must be pointed out that the small size of the fish larvae caught during this study could be related to the fact that, according to Rodríguez (2008), many species in the region would be at the beginning of their spawning period. Thus, many of the species whose larvae were caught in this study would reproduce mainly during downwelling dominant conditions. This is one of the strategies that may follow fish species in regions of coastal upwelling to avoid or reduce the offshore transport of their offspring by the Ekman transport associated with coastal upwelling (Parrish *et al.*, 1981).

In summary, the late winter (February and March) 2012 was anomalous in that the average values of the upwelling index indicated relatively strong upwelling.

However, during the time of the cruise the average values of the upwelling index indicated weak downwelling, supported by the offshore–onshore distribution of larval size of the species that reproduce over the slope. Fish larvae showed a depth stratified vertical distribution, both day and night, although the Larval Fish Community (LFC) was not structured in the vertical plane. Fish larvae seem not to perform DVM although some fish species showed significant OVM. In regions of coastal upwelling and in the absence of DVM, the location of fish larvae in the water column is crucial for their cross-shelf distribution, as they cannot move between the stratified currents of these regions to maintain their cross-shelf position. Also in these regions, the wide vertical distribution shown by larvae of the offshore spawning species could be an adaptation to ensure that some larvae reach the inshore nursery areas, either transported by the surface onshore flow associated with coastal downwelling (larvae located close to the surface) or by the deep onshore flow associated with coastal upwelling (deeper larvae).

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